DREDGED MATERIAL RESEARCH PROGRAM

TECHNICAL REPORT D-77-36

PRIMARY PRODUCTIVITY OF MINOR MARSH PLANTS IN DELAWARE, GEORGIA, AND MAINE

by

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Final Report

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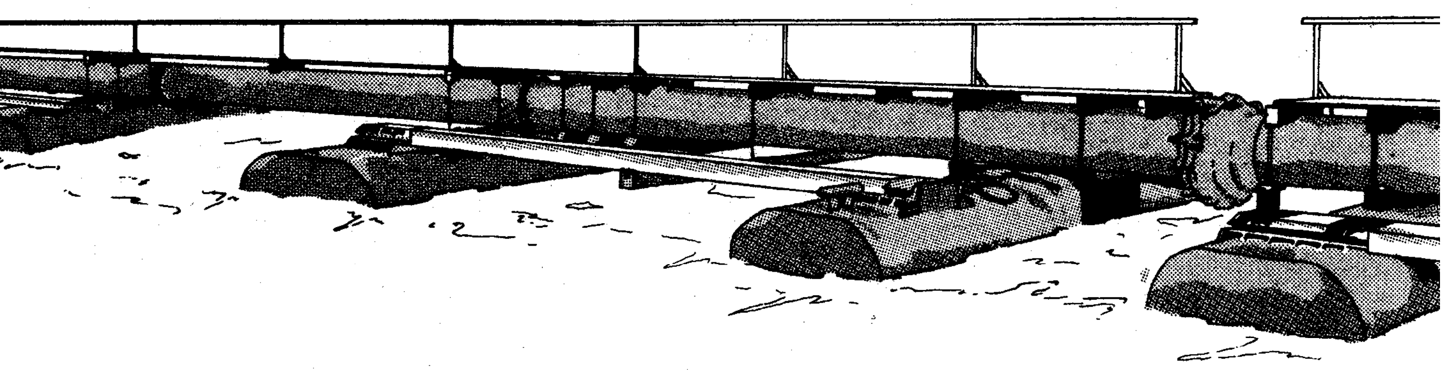

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Errata Sheet

No. 1

PRIMARY PRODUCTIVITY OF MINOR MARSH PLANTS IN DELAWARE, GEORGIA, AND MAINE

Technical Report D-77-36

November 1977

1. Pages D4, D7, and D11 (on microfiche): Sampling dates of 3 June 1975, 29 July 1975, and 24 September 1975 should read 3 June 1974, 29 June 1974, and 24 September 1974, respectively.

2. Page 15, Figure 3, figure title should read: Figure 3. Geographic location of collection sites in Georgia: A - *Distichlis spicata, Iva frutescens, Spartina patens,* and *Sporobolus virginicus;* and B - *Borrichia frutescens* and *Spartina cynosuroides*

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30 November 1977

SUBJECT: Transmittal of Technical Report D-77-36

TO: All Report Recipients

1. The technical report transmitted herewith represents the results of one of the research efforts (work units) under Task 4A (Marsh Development) of the Corps of Engineers' Dredged Material Research Program (DMRP). Task 4A is part of the Habitat Development Project of the DMRP and is concerned with developing, testing, and evaluating the environmental, economic, and engineering feasibility of using dredged material as a substrate for marsh development.

2. Net annual aerial primary productivity is a commonly used descriptor of the value of salt marshes. Primary productivity here is considered the rate at which the sun's energy is stored as green tissue available to the ecosystem. This work unit (4A01A1) deals with several key aspects of the primary productivity of selected minor marsh plants in Maine, Delaware, and Georgia. Specifically, the topics of plant density, biomass, detrital flux, mortality, and comparisons of techniques for measuring productivity are addressed. The information derived in this study should be of direct value in evaluating the relative ecological importance of potential dredged material disposal sites. The information provided will also be exceptionally useful in the design of new marsh habitats on dredged material.

3. Work Unit 4A04A1 is one of several research efforts designed by the DMRP to document marsh productivity and the factors which influence that productivity. Closely related work units are 4A04A2, which deals with marsh plant substrate selectivity and underground biomass production; 4A04B, which addresses the productivity of minor marsh species in Louisiana; and 4A05 in which a simulation model to predict salt marsh productivity was developed. In a less intensive study, Work Unit 4A20 will provide a general evaluation of salt marsh productivity of the Pacific coast of the United States. Additional supportive and comparative data will be forthcoming with the final analysis of the results of field studies at Windmill Point, Virginia, (4A11); Buttermilk Sound, Georgia, (4A12); Apalachicola, Florida, (4A19); Bolivar Peninsula, Texas, (4A13); Pond No. 3, San Francisco Bay, California, (4A18); and

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Miller Sands, Oregon, (4B05). Together these research products provide the Corps with a comprehensive basis for sound management decisions regarding dredged material in salt marsh habitats.

JOHN L. CANNON
Colonel, Corps of Engineers
Commander and Director

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18. SUPPLEMENTARY NOTES

Appendixes A, B, C, and D are reproduced on microfiche and are enclosed in an envelope attached to the inside of the back cover.

19. KEY WORDS (Continue on reverse side if necessary and identify by block number)

Coastal marshes	Maine
Delaware	Marsh plants
Dredged material disposal	Plant growth
Georgia	Productivity

20. ABSTRACT (Continue on reverse side if necessary and identify by block number)

This report summarizes the importance of common species of salt marsh plants inhabiting wetlands of the eastern U. S. coast. An evaluation of the ecological significance of the plants is based on their rates of primary production, mortality, and contribution of detritus to the estuarine dependent systems. The data are important in reaching decisions relative to the deposition of dredged material in these coastal wetland systems.

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* Appendixes A, B, C, and D are reproduced on microfiche and are enclosed in an envelope attached to the inside of the back cover.

EXECUTIVE SUMMARY

Over the past two centuries, many of our nation's wetlands have been filled or drained for agricultural, industrial, or residential expansion. During the last two decades, the ecological importance of wetlands has been a focal point for coastal research. Numerous attempts have been made to classify these wetlands in terms of fish and wildlife habitats, i.e. according to aesthetic or subjective values. Wetland marsh areas have been defined as areas that are inundated or recharged with sufficient frequency to be capable of supporting herbaceous vegetation that requires or tolerates the saturated soils for growth or reproduction under normal circumstances. Numerous criteria have been assessed in considering the importance of these wetlands. Hydraulics and stream order, the depth, frequency, and duration of flooding, the capacity for release and assimilation of materials, the regional micro-climatology, the fish and wildlife habitat, the frequency and duration of saturation, and the primary productivity above ground and below ground of the plants, all are parameters that have received attention relative to establishing marsh value for management decisions. Although a number of scientific proofs have been offered relative to wetlands values, the most credible factors concern the relationship between marsh plant production and the aquatic fish and invertebrate production. Past studies have focused on wildlife and natural history studies of the fauna of the coast. More recently, scientists have begun to quantify the growth or primary production of plants since this primary production of plants is the basis for the entire coastal estuarine food web.

Proceeding on the assumption that these coastal marshlands do have an ecological value, some marshes must be more valuable than others. There also must be ways of assessing the value of marshes so that management decisions relative to their conservation may be made. This evaluation, however, must be quantitative, scientific, objective and reasonable as a criterion for deciding which marshes should be protected and preserved and which ones should be exploited. An ecological rating system that relies on natural resource management principles and personnel to make the measurements would seem to be appropriate to quantify the importance of various types of wetlands.

Research efforts in the past two decades relative to the primary productivity of marsh plants have focused on the plant, *Spartina alterniflora*. Management decisions relative to marsh were made on a data base of *Spartina alterniflora*. When other species of plants were considered relative to marsh perturbation, they were always considered less important or "minor species" because of the lesser areal extent when contrasted to *Spartina alterniflora*. A thorough review of the scientific literature, however, revealed that any management decisions based on the primary productivity of the "minor species" of marsh plants heretofore had been based on mythology and not upon competent scientific research. Consequently, the purpose of this study was to evaluate the importance of the primary productivity of a variety of species of salt marsh plants commonly occurring along the eastern coast of the United States relative to the disposition of dredged material. The results are intended to assist in management decisions relative to marsh values which in turn suggest the kinds of marsh which can be altered or disturbed or used as sites for deposition of dredged material during waterway maintenance activities.

Using similar methodology, the primary production of the salt marsh plants common to the Atlantic coastal zone was determined in Delaware, Georgia, and Maine over a 2 yr period. Parameters determined included aerial plant density, biomass, detritus flux, estimated net primary productivity, and mortality. The elevation, above or below mhw, at which each plant exists was determined. An evaluation of the net aerial primary production estimation methodology was also considered.

At the outset of the study, it was considered that *Spartina alterniflora* was the most prolific primary producer in the east coast marshes. It was also assumed that marsh primary production decreased with increasing latitude. Studies heretofore conducted during different years using different methodologies had suggested a dramatic decrease in primary production in the more northerly latitudes contrasted with the southern latitudes. The results of this study indicate that *Spartina patens* in Maine and *Spartina cynosuroides* in Georgia are among the most productive plants along the eastern coast. This is contrary to the belief that *Spartina alterniflora* is the most productive marsh plant in Georgia. *Juncus gerardii* on the creekbank in Maine and *Distichlis spicata* and *Spartina patens* in Georgia all had somewhat lesser primary production than *Spartina patens* in Maine and *Spartina cynosuroides* in Georgia. In ranking these species, production decreased among the plants considered. Those of the lowest production included *Sporobolus virginicus* in Georgia and *Juncus gerardii* on the highmarsh in Maine. The primary production ranged from over 6,000 $g/m^2/yr$ to 600 $g/m^2/yr$. An analysis of the four parts of this report reveals the tremendous significance of the formerly known "minor species" as important sources of primary production and detritus for the sustenance of the estuarine ecosystem. Consideration of the density of stems per unit area reveals that the greatest stem density occurred in the plants from Maine. Evaluation of the tidal range in which the plants live revealed that none of the plants from Delaware or Georgia (except *Spartina cynosuroides*) live below mhw; however, several of the plant species in Maine occur below mhw.

The report summarizes a computation of each of the measured variables and relates the results to earlier literature. The data document a highly productive nature of the "minor marsh plant species", formerly considered to be minor simply because of their relatively lesser abundance and supposedly lower productivity. The data reveal that in terms of ecological values one must consider the estuarine macrophytes studied *(Borrichia frutescens, Distichlis spicata, Iva frutescens, Juncus gerardii, Phragmites communis, Spartina alterniflora, Spartina cynosuroides, Spartina patens,* and *Sporobolus virginicus)* as valuable natural resource components when planning for the deposition of dredged material. In terms of detritus production, the main energy source for estuarine metabolism, the contribution of these minor plants is very significant and deserving of attention when making management decisions. Although earlier data had suggested the latitudinal differences, the results revealed that there was no evidence to suggest that a difference in the length of the growing season had a pronounced effect on the maximum values of the parameters measured. Although the environmental metabolism and decomposition of the dead material was greater in the southern latitudes, the primary production appeared to be more equal throughout the regime studied. There are differences in the climate, soil properties, tidal activity, and other biotic and abiotic factors that act on any single site; therefore differences in environmental metabolism account for the differences in primary production of each minor marsh plant considered. Since primary production is one of the more important parameters of the marsh in terms of an ecological evaluation, intensive consideration of the aerial primary production reported herein, and the below-ground primary production (in a companion report by J. L. Gallagher et al.), become essential ingredients in competent environmental management decision making.

PREFACE

The work described in this report was performed under Contract No. DACW39-73-C-0110, entitled, "Research Study for Determining Production of Minor Marsh Plant Species and Their Substrate Selective Properties," dated June 1973 between the U. S. Army Engineer Waterways Experiment Station (WES), Vicksburg, Mississippi, and the University of Georgia, Marine Extension Service, Brunswick, Georgia. The research was sponsored by the Dredged Material Research Program (DMRP), Environmental Effects Laboratory (EEL), WES.

Authors of the report were Dr. Robert J. Reimold and Mr. Rick A. Linthurst. Messrs. F. Gerald Plumley, Patrick C. Adams, and Gregory A. Kramer and Ms. Helen D. Walker assisted with the research.

A sincere thanks is expressed to the following individuals (funded from other sources) who contributed their untiring efforts to the successful completion of the project: Dianne H. Adams, Hannah D. Brown, Charles J. Durant, Ann O. Fornes, Lorene T. Gassert, Michael A. Hardisky, James J. Kowalchuk, Christine L. Langner, Allyson S. Linthurst, William J. Pfeiffer, Jacquelin B. Ulmer, Owen M. Ulmer, Jr., James A. Vernon, Shirley A. Walker, and Victoria C. Wray. The authors also thank Dr. Kent S. Price, Associate Dean, and the staff of the College of Marine Studies, University of Delaware, Lewes, Delaware, and Dr. William B. Kinter and Mr. Hal Church and the staff of the Mt. Desert Island Biological Laboratory, Salisbury Cove, Maine, for laboratory space and logistics support in connection with collection of the Delaware and Maine samples, respectively.

The support and contributions of the Sapelo Island Research Foundation, Inc., were essential for the conduct of this research.

This report was prepared for the Habitat Development Project (Dr. Hanley K. Smith, Manager) under Work Unit 4A04A1, part of Task 4A: Marsh Development. Dr. John Harrison, Chief, EEL, provided general supervision. EEL botanists, Dr. Luther F. Holloway and 1LT Terry Huffman, monitored the study.

COL G. H. Hilt, CE, and COL J. L. Cannon, CE, were directors of WES during the period of this study. Mr. F. R. Brown was Technical Director.

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PRIMARY PRODUCTIVITY OF MINOR MARSH PLANTS IN DELAWARE, GEORGIA, AND MAINE

PART I: INTRODUCTION

The extensive nature of this study has resulted in reams of information. To make the material more comprehensive and understandable, it has been segmented. The first major section deals with the geographic details of the study and the aerial plant density and biomass data from the collection sites in Delaware, Georgia, and Maine. The second section summarizes the detritus flux, mortality, and estimated net primary productivity of the plants. The third section discusses the problems associated with primary production estimation and considers the results of this study in light of several methodologies commonly employed for production measurements. The ancillary data related to climatological data, tidal data, monthly mean values for living biomass, dead biomass, live:dead ratios, living stem densities, individual stem weights, percent dead, instantaneous rate of detritus flux, mortality, and estimated primary productivity all are appended to the report. Some information is repeated so that each section may be considered independently.

General data are presented in the appendices as follows: Appendix A - Monthly Climatological Data; Appendix B - Tidal Data; and Appendix C - Monthly Mean Values for Angiosperms Sampled.

PART II: BASELINE INFORMATION ON AERIAL PLANT DENSITY AND BIOMASS FOR SELECTED ESTUARINE ANGIOSPERMS

Introduction

1. The importance of the salt marsh-estuarine ecosystem has been well documented in the literature (Odum 1961, Teal 1962, Odum and de la Cruz 1967, Cooper 1969, Sweet 1971, Gosselink et al. 1974). The coastal zone of the United States appears to be one of the most economically and ecologically productive regions in the nation (Reimold 1976.) In addition, the salt marsh-estuarine ecosystem has been shown to function as a buffer zone between tidal waters and land during storms, as a nursery ground for a variety of marine organisms, and as an energy source for the estuary itself. However, with the intensification of coastal zone usage (shore-line development, fisheries, aquaculture, and mineral exploration), it is necessary to gain a more complete understanding of the salt marsh ecosystem.

2. A majority of studies of the estuarine system energetics have been primarily based on studies of *Spartina alterniflora* (Smalley, 1958; Morgan, 1961; Odum, 1961; Teal, 1962; Good, 1965; Stroud and Cooper, 1968; Johnson, 1970; Kirby, 1971; Durand and Nadeau, 1972; Keefe and Boynton, 1973; Wiegert et al., 1975). Teal (1962) assimilated the earlier works of many researchers in the southeastern salt marshes and produced a conceptual model of energy flow and the magnitudes of cyclic fluxes. More recently, these studies have turned to mathematical model studies incorporating algal activity information, nutrient cycles, aerial harvest information, and below-ground biomass activity (Pomeroy et al., 1972; Day et al., 1973; Reimold, 1974; Wiegert et al., 1975).

3. As Federal, State, and private interests continue to exert efforts toward a more complete understanding of the estuarine system, energetics studies resulting in models designed to predict the outcome of perturbations will continue. The purpose of this study was

to acquire baseline seasonal density and biomass estimates of the plant species often ignored due to their relatively small areal extent along the eastern shore of the United States. This information is basic to all energetics studies if a complete analysis of the salt marsh-estuarine system is to be made possible.

Methods

4. Saline marsh sites in Maine, Delaware, and Georgia were selected for study (Figures 1 - 3). Selection criteria included a broad latitudinal range (31°19' to 44°34'), logistically feasible access within the time allowed for collection and preparation of samples (1 week), and laboratory facilities which could be utilized for immediate preparation of the samples. Marshes were selected which had similar vegetative diversity with monospecific stands of the angiosperms to be evaluated. Sites were subjectively selected in order to limit the effect of varying environmental conditions.

5. Optimum quadrat size used for sampling aerial plant material was determined in August 1973 according to the method of Wiegert (1962). The plant species chosen for investigation, the states where they were sampled, and the quadrat sizes used are shown in Table 1.

6. *Juncus gerardii* stands in Maine were referred to as creekbank where the plants were growing on a steep slope above the *Spartina alterniflora* and as highmarsh where the plants were growing on a relatively flat site landward of the creekbank plants. Similar differentiation was employed in the *Spartina alterniflora* stands. The *Juncus gerardii* stands in Maine were mixed with another rush nearly identical in growth form, *Juncus balticus*. Because of the periodic absence of fruiting or flowering structures necessary for separating the two during sampling, this stand was treated as a monospecific stand of *Juncus gerardii*.

7. A majority of the plant species sampled had a limited geographic distribution and were therefore unavailable for sampling in all states. *Phragmites communis* and *Spartina cynosuroides* had a

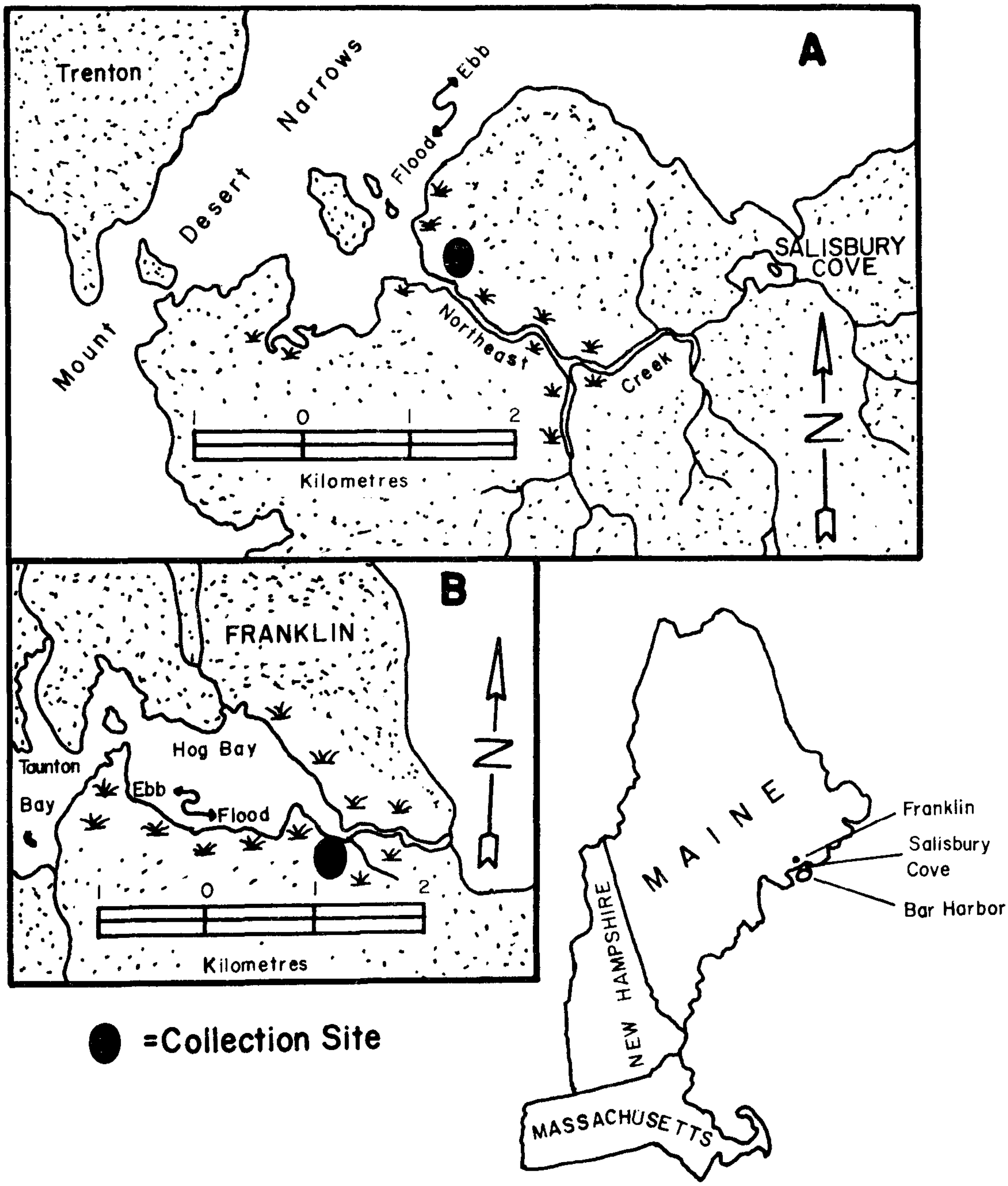


Figure 1. Geographic location of collection sites in Maine; A - *Juncus gerardii* (creekbank and highmarsh) and *Spartina alterniflora* (creekbank); B - *Spartina alterniflora* (highmarsh), *Spartina patens*, and *Carex* sp.

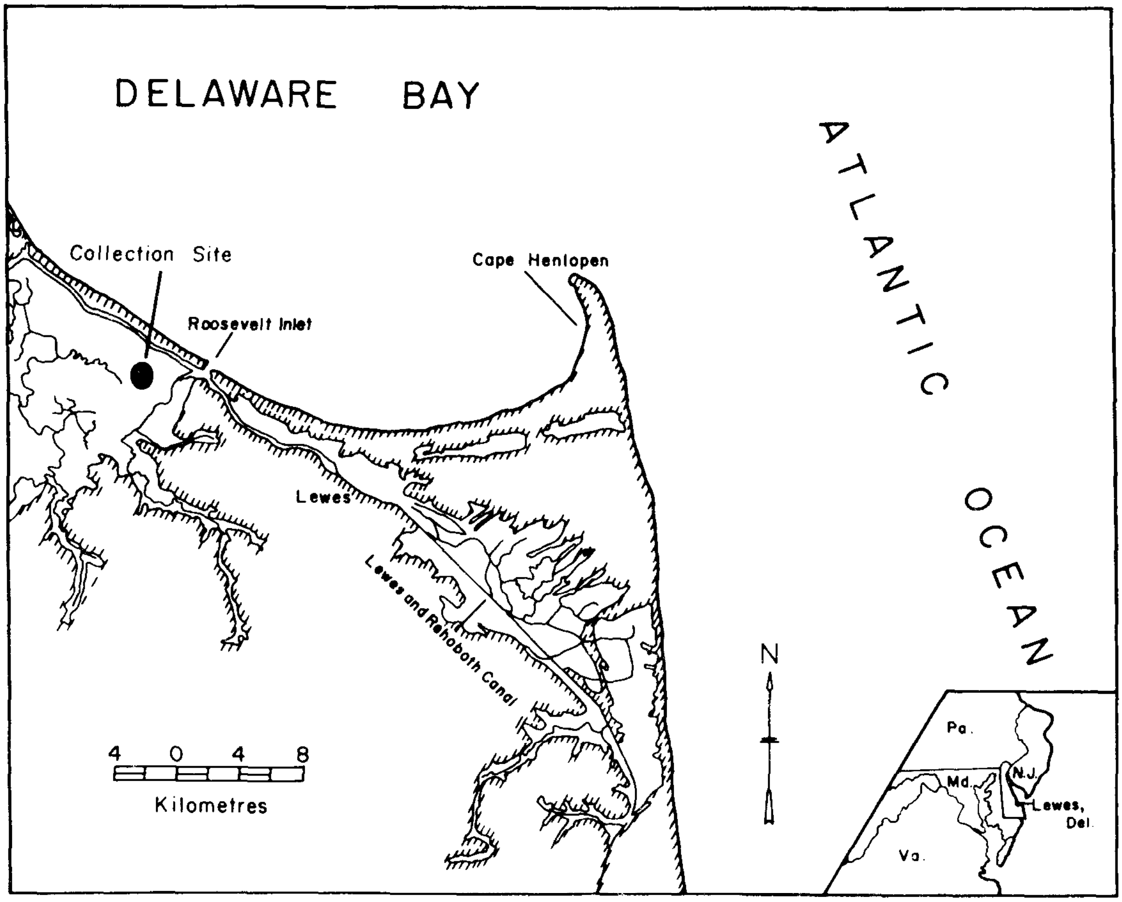


Figure 2. Geographic location of collection sites in Delaware

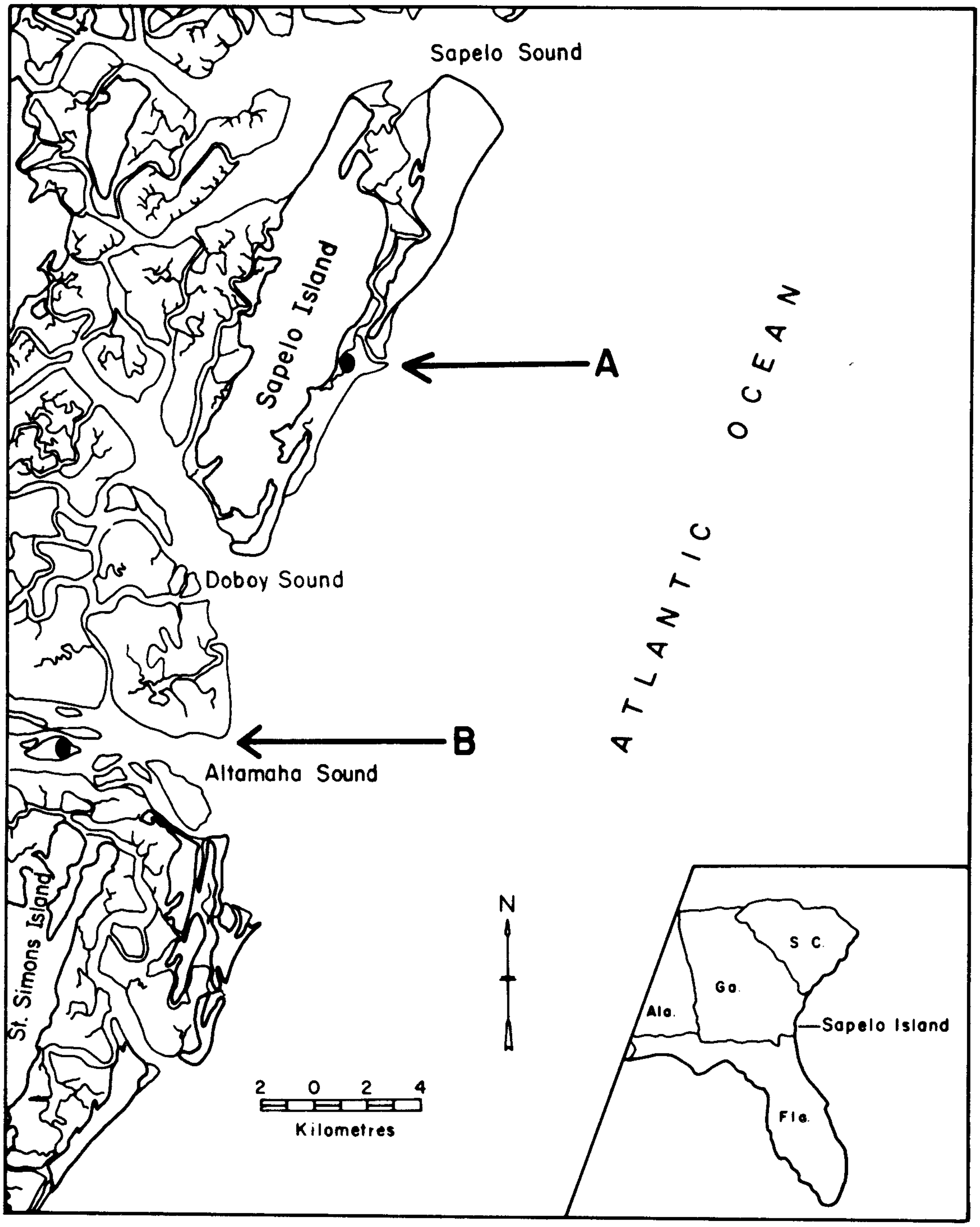


Figure 3. Geographic location of collection sites in Georgia; A - *Distichlis spicata, Iva frutescens, Spartina patens,* and *Sporobolus virginicus;* B - *Borrichia frutescens;* C - *Spartina cynosuroides*

Table 1

Angiosperms Evaluated, Their Geographic Location, and Sample Quadrat Size for Collection Sites

Angiosperms	Location[a]			Quadrat size m^2
Borrichia frutescens			G	0.50
Distichlis spicata		D	G	0.01
Iva frutescens		D	G	0.50
Juncus gerardii[b]	M			0.01
Juncus gerardii[c]	M	D		0.01
Phragmites communis		D		0.50
Spartina alterniflora[b]	M			0.10
Spartina alterniflora[c]	M			0.10
Spartina cynosuroides			G	0.50
Spartina patens	M	D	G	0.01
Sporobolus virginicus			G	0.01

[a]M = Maine; D = Delaware; G = Georgia
[b]Creekbank
[c]Highmarsh

broader latitudinal growth range than sampled; however, they were not found in an area where sampling could be done based on the criteria discussed earlier. Finally, *Spartina alterniflora* was found in all locations but sampled only in Maine. Biomass evaluations for *Spartina alterniflora* in the southeastern and middle Atlantic coastal regions were already well documented in the literature (de la Cruz 1973, Hatcher and Mann 1975, Reimold et al. 1975, Mendelssohn and Marcellus 1976, and Gallagher et al. In press). Therefore, this angiosperm was investigated only in Maine where literature values were unavailable.

8. Contiguous paired plots as described by Wiegert and Evans (1964) were employed for the collection of the aerial plant material and litter. Stainless steel hand pruners or dissecting scissors were utilized for harvesting. Dissecting scissors were used on all plots of 0.1 m^2 or smaller to increase the accuracy of the harvest by potentially decreasing experimental error in these small quadrats. Five samples were taken simultaneously within each stand, at all locations, and at 56-day intervals from the initiation of the study on 27 August 1973 through its termination on 25 August 1975 in Delaware and Georgia. *Iva frutescens* and *Sporobolus virginicus* sampling was not initiated until 3 June 1974 and continued until the termination of sampling at the other locations. Because of the severity of the winter and the impossibility of accurate sampling during months when the Maine site was covered with ice and snow, sampling in Maine was restricted to late spring, summer, and early fall. In addition, one 28-day sampling interval was necessary to approximate initiation time of spring plant growth in Maine.

9. Plant material harvested in the field was separated into live and dead components and placed in polyethylene bags of sizes ranging from 0.9 ℓ to 208.0 ℓ dependent upon the amount of material present. *Iva frutescens* was always separated into living and dead components in the field due to the brittle nature of the dead portions of the living stems which when mixed with standing dead tissue were inseparable. Evidence of green material on the stem dictated the selection of living plants, and material with an absence of green

coloration was assessed to be dead. The samples were returned to the preparation laboratory at the respective sites immediately following the field sampling. Here they were weighed using a Model 2197 Ohaus 5-kg balance with a sensitivity of ± 0.5 g to determine fresh weight values to the nearest 1.0 g. Dead portions of the living plants were stripped off and weighed separately. The necessity of subsampling to evaluate dry weights was determined based upon the amount of material that would adequately fill a 0.9-ℓ jar. Samples harvested in Delaware and Maine were packaged and transported by air to Georgia where they were placed in jars and dried in a mechanically convected forced draft oven at 100° C to a constant weight. All samples were removed from the oven when dry and weighed on a Mettler Model P11, 11-kg-capacity balance with a sensitivity of ± 0.05 g. Subsample data were expanded to include the complete harvest fresh weights, and subsequently all data were expanded to a square metre basis.

10. All harvest data analyses were based on dry weight information. Natural logarithmic transformations were used for graphical presentation to equalize the variances of all values that had a general tendency to increase with increasing values of the Y parameters. Transformations were also used to present information graphically on similar or, when possible, identical scales. The physiognomy of the plant species evaluated was such that a wide range of values within any parameter was observed, making it impossible to plot untransformed information on a comparative scale. Because of the natural logarithmic transformation, the value of one was added to all values shown graphically to avoid unpresentable zero values. Statistical evaluations were completed according to Snedecor and Cochran (1967).

11. The Maine data graphically portray projected minima where applicable, based on observations during periods when quantitative data were unobtainable. The dead material components show no projections during periods when samples were not collected, since there were no means of adequately assessing this parameter when quantitative data were unavailable. In addition, the frozen, often ice or snow covered marsh led to the assumptions that decomposition was negligible

during these periods and that the significant increases or decreases in dead material amounts were monitored by the data collected early or late in the season.

Results and Discussion

Borrichia frutescens

12. A seasonal pattern in *Borrichia frutescens* living aerial biomass was evident (Figure 4) with declining live material during the winter and maximum biomass during the summer. The maximum biomass values obtained corresponded to times of flower initiation and development. The range of *Borrichia frutescens* dead biomass was considerably smaller than that of the standing living biomass (Figure 4) and no clear seasonal trend was apparent for this component. Seasonality of dead material might be evident if the leaves of the woody *Borrichia frutescens* remained attached to the plant or remained as litter in the surrounding area after abscission. However, this material rapidly disappeared from the localized area due to periodic tidal flushing. Live stem densities (Figure 4) also indicated little seasonal change although maximum stem counts consistently occurred in late spring (Figure 4).

13. There were nearly constant amounts of dead material per stem throughout the 2 yr evaluation period while the dry weights of individual live stems showed an increase in biomass during the summer months (Appendix C).

Distichlis spicata

14. Living aerial biomass of *Distichlis spicata* in Delaware had a more extreme range of values than did the Georgia stand (Figure 5). The colder weather during the winter months in Delaware was assumed to be the major factor in creating this difference. Maximum summer living biomass was higher in Delaware (1142 g/m^2) than that computed for Georgia (458 g/m^2) with peaks in August or September in both locations although the Delaware maximum was quite variable. Typical summer maximum values were approximately 100 g/m^2 greater in

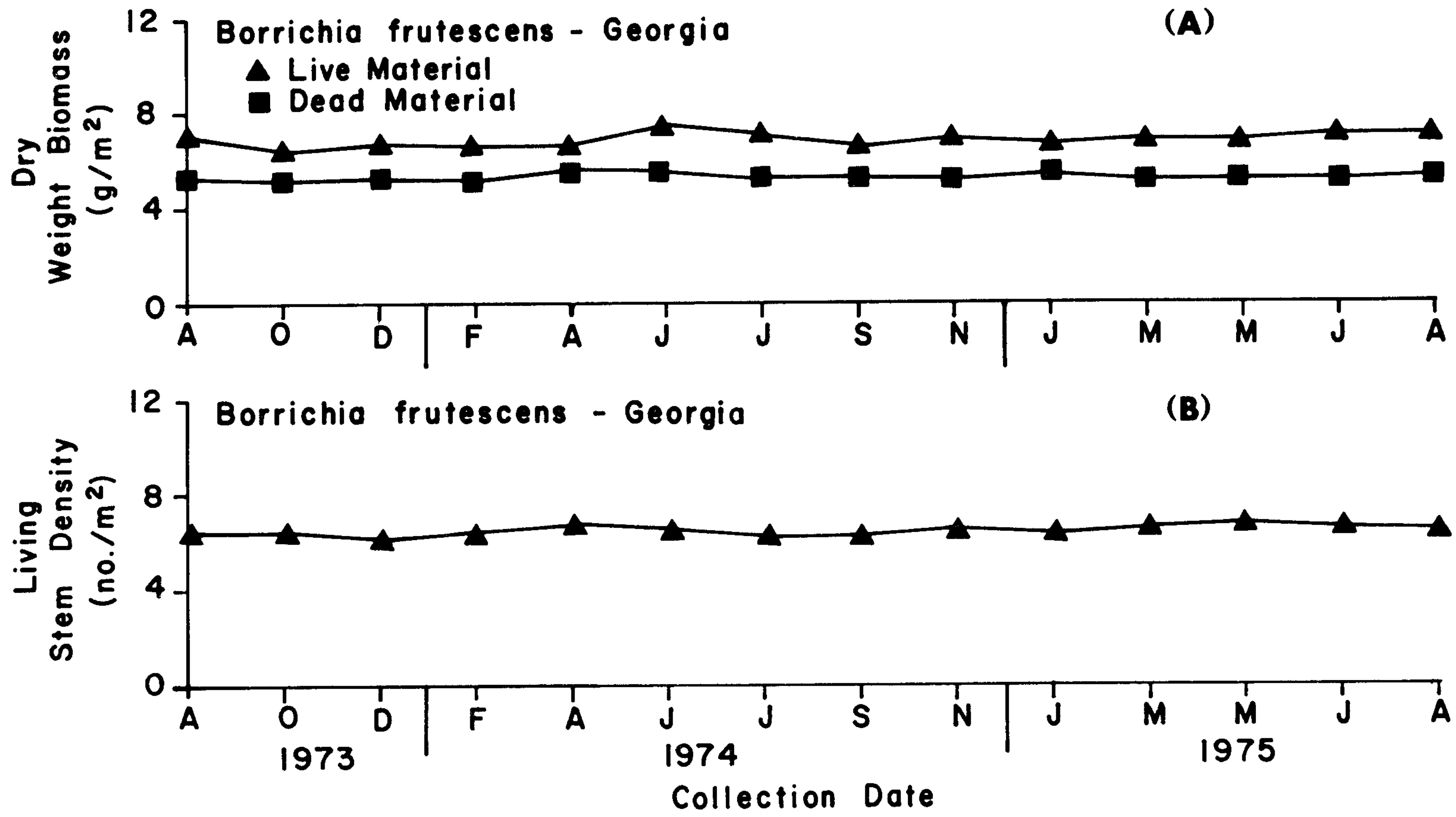


Figure 4. Natural logarithmic plots of living and dead dry weight biomass (mean $\pm$ S.E.) and living stem densities for *Borrichia frutescens*. Standard errors are not shown when smaller than the size of the symbol

Delaware than in Georgia. The increased variability noted during the winter in the Delaware samples (Figure 5) was related to the quadrat siz used for harvesting. During these months, there were insignificant amounts of living material present in the Delaware marsh, and the small quadrat size resulted in increased heterogeneity of the samples. Although the natural logarithmic transformations were utilized to equalize the variance, in this instance, the procedure tended to make the smaller biomass variances appear more extreme. The two locations demonstrated maximum and minimum dead biomass on the same collection dates and similar ranges (February and August, respectively, Figure 5). The variation in magnitude of dead material in Georgia was the same as the range of dead material in Delaware and nearly two times that of the living biomass in Delaware. This phenomenon suggested a substantial litter base in the Georgia *Distichlis spicata* and either an unstable community where litter accumulation was a dominant factor or rapid turnover of living biomass was occurring.

15. Stem densities were relatively constant for *Distichlis spicata* in Georgia throughout the year. High densities in Delaware (Figure 6) corresponded to the warmer summer temperatures. The Delaware stand was more dense at its peak than the Georgia stand (6160 and 2300 stems/m^2, respectively), and visual observation of the two stands prior to the initiation of sampling suggested no such extreme difference in density. Weights of individual living stems were greatest in late summer for both *Distichlis spicata* stands, with the Delaware stems being generally lighter in weight (Appendix C). The estimated percentage of the living plant which was dead during the harvest intervals indicated that either the Georgia plants lived longer than those in Delaware or that new shoots were initiated more frequently (Appendix C). Based on the amount of dead material present in Georgia, it appears more likely that new shoots were initiated more frequently and over a longer period of time. This observation then suggests that the mortality rate was greater in Georgia as opposed to the earlier suggestion that individual stems might live longer in Georgia than those in Delaware.

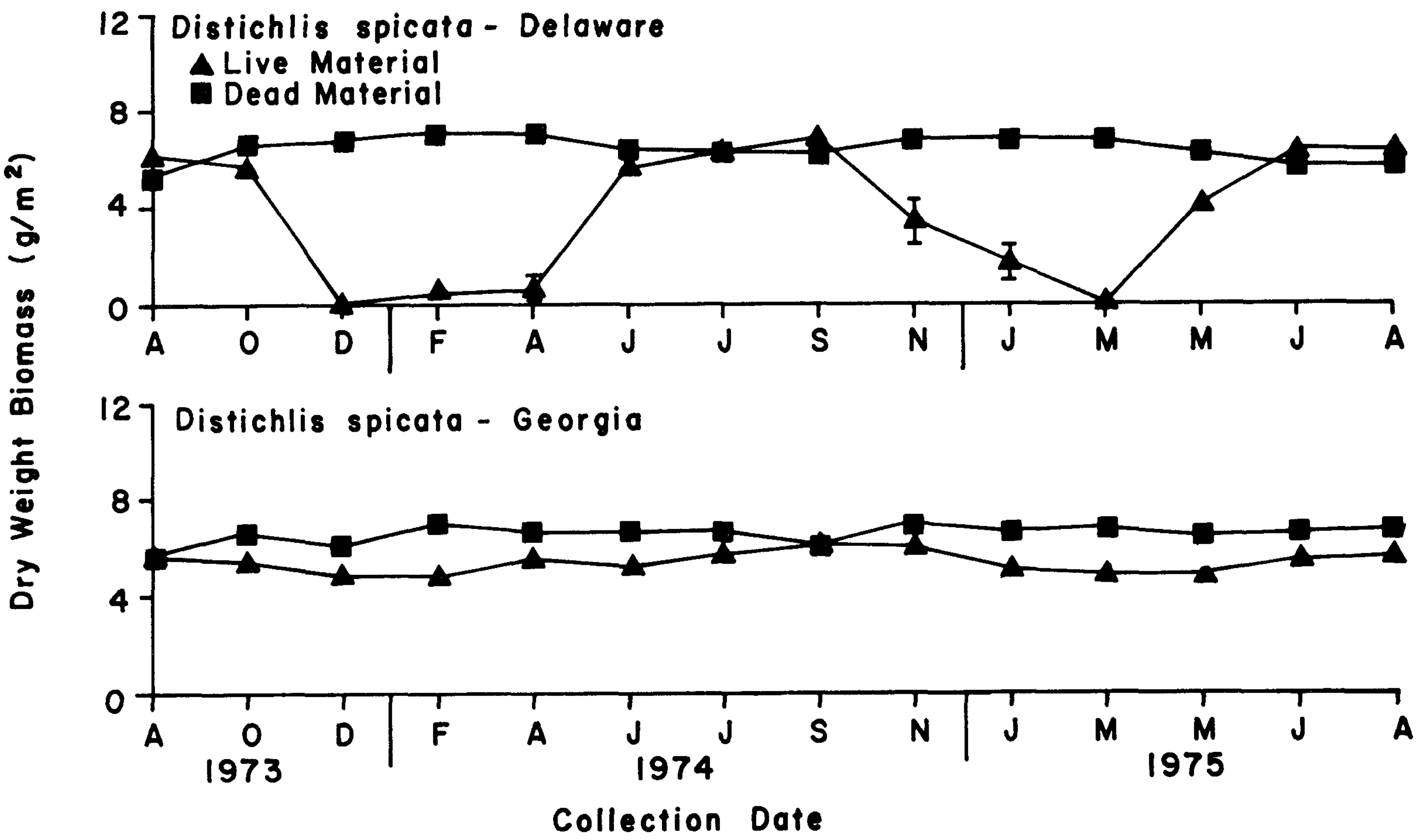


Figure 5. Natural logarithmic plots of living and dead aerial dry weight biomass (mean ± S.E.) for *Distichlis spicata*. Standard errors are not shown when smaller than the size of the symbol.

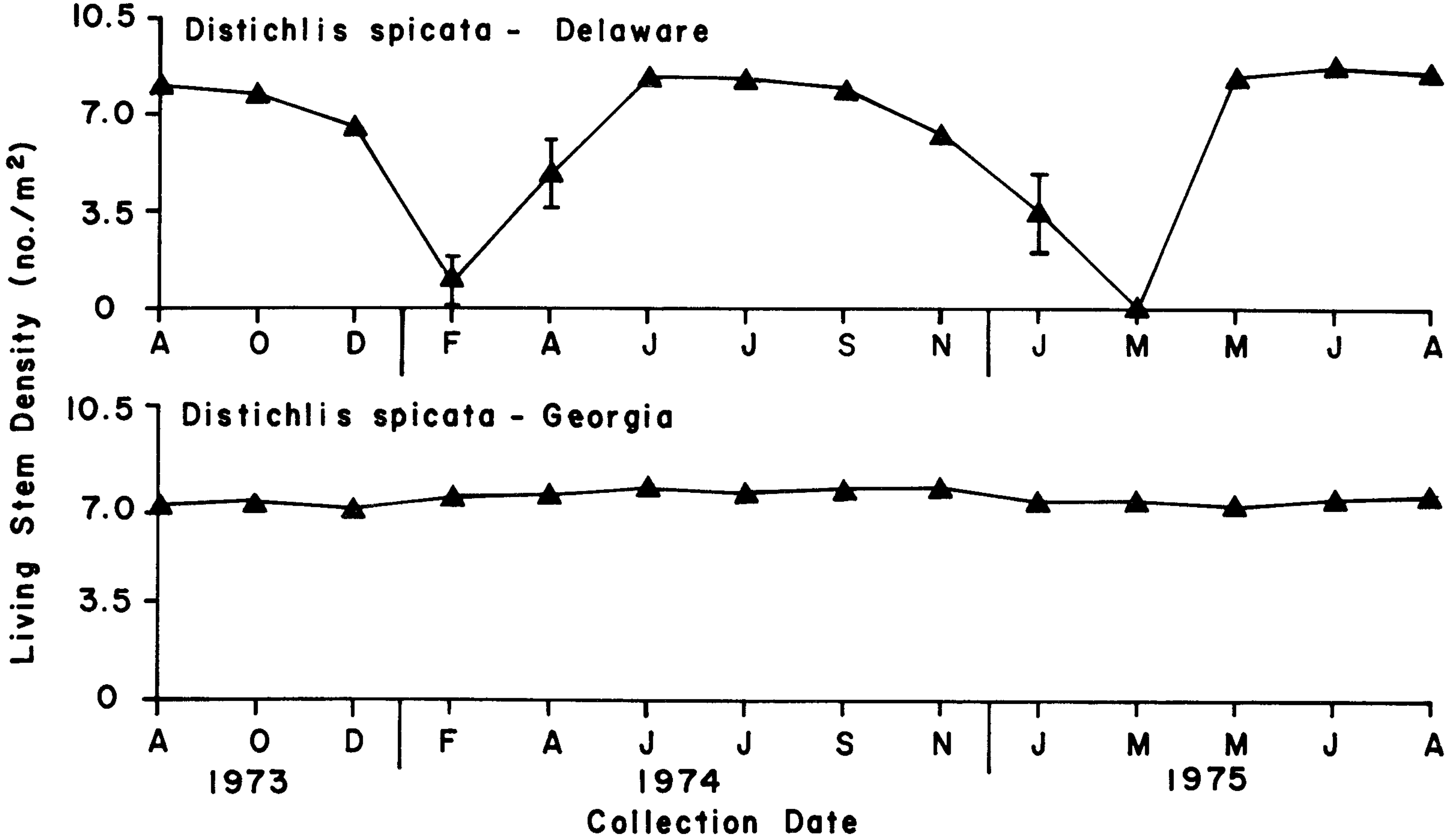


Figure 6. Natural logarithmic plots of living stem density (mean ± S.E.) for *Distichlis spicata*. Standard errors are not shown when smaller than the size of the symbol.

Iva frutescens

16. The clumped distribution and shrubby growth form of *Iva frutescens* caused greater component variance than with any other species sampled. The *Iva frutescens* from Georgia and Delaware displayed nearly identical ranges of living biomass (Figure 7). The major contribution of *Iva frutescens* to the estuarine system was the leaf and flower material lost from the plants during the growing season, as with *Borrichia frutescens*. The dry weight of dead *Iva frutescens* in the Delaware marsh was both greatest and smallest in late fall and early winter. Dead biomass of *Iva frutescens* in Georgia was smallest in the spring and greatest in August (Figure 7). Neither stand displayed evidence of litter accumulation. The difficulty experienced in separating live from dead stem material was similar to that of *Borrichia frutescens* samples where stems had to be broken to discern this difference. The stem radius on this plant was three to four times greater than that of *Borrichia frutescens*, which made harvesting the stems at ground level difficult.

17. Stem density data (Figure 8) indicated a greater number of living *Iva frutescens* stems in Delaware than collected in Georgia (Figure 8). Although seasonality of density appeared more evident in Georgia than in Delaware, stem density determination was often difficult due to the growth form of the plant and was therefore subject to question. The *Iva frutescens* in Delaware was the only angiosperm at that location which had a nonzero winter stem density or living biomass component.

Juncus gerardii

18. The amount of living *J. gerardii* present in Delaware declined earlier in the season than other plants sampled (Figure 9). *Juncus gerardii* live biomass showed an increase during the winter months to a peak that occurred early in the summer. The Maine sites were more difficult to evaluate because of the varied sampling frequency described earlier; however, a seasonal pattern was discernable.

19. The live *Juncus gerardii* in the Maine creekbank stand

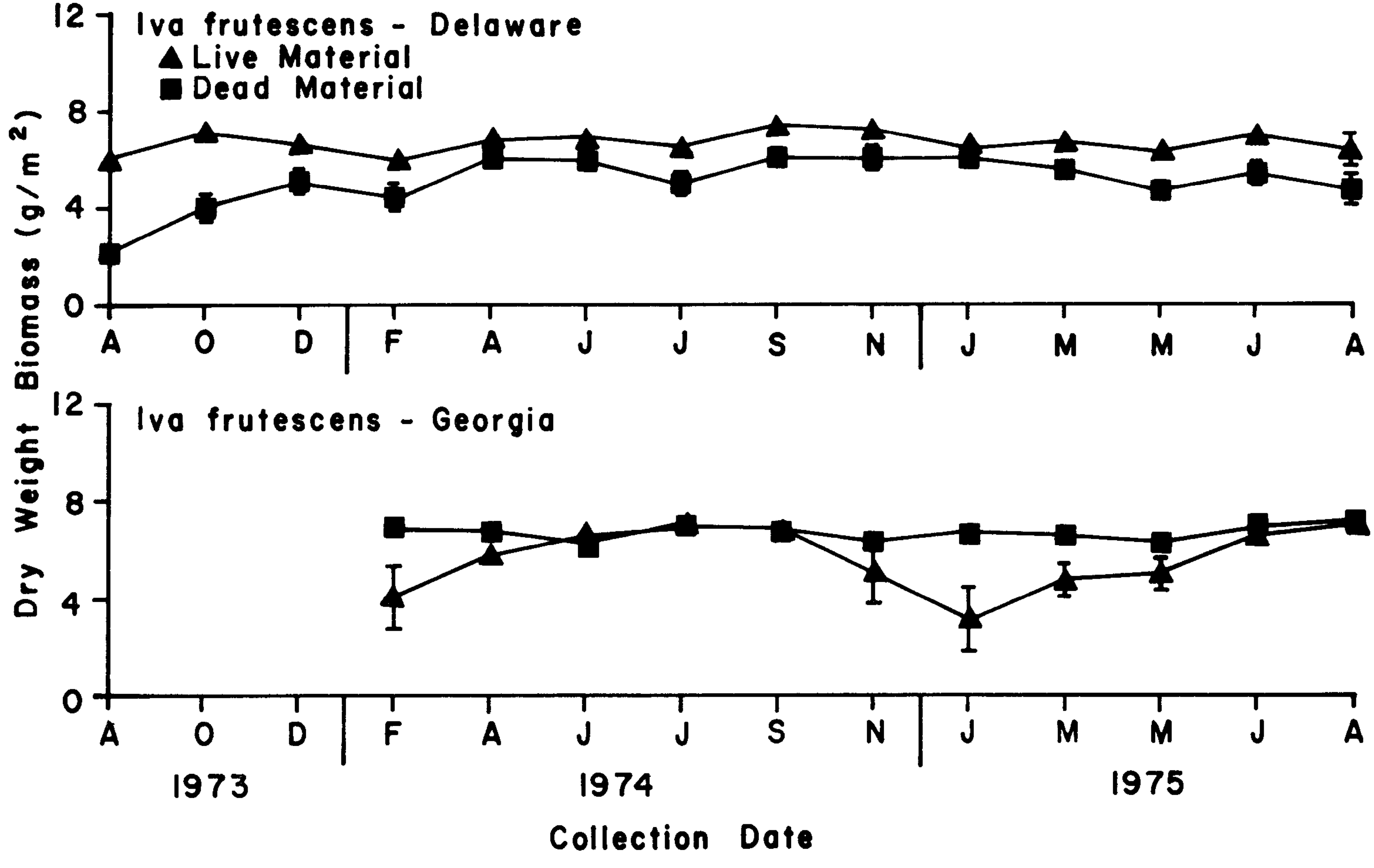


Figure 7. Natural logarithmic plots of living and dead aerial dry weight biomass (mean ± S.E.) for *Iva frutescens*. Standard errors are not shown when smaller than the size of the symbol.

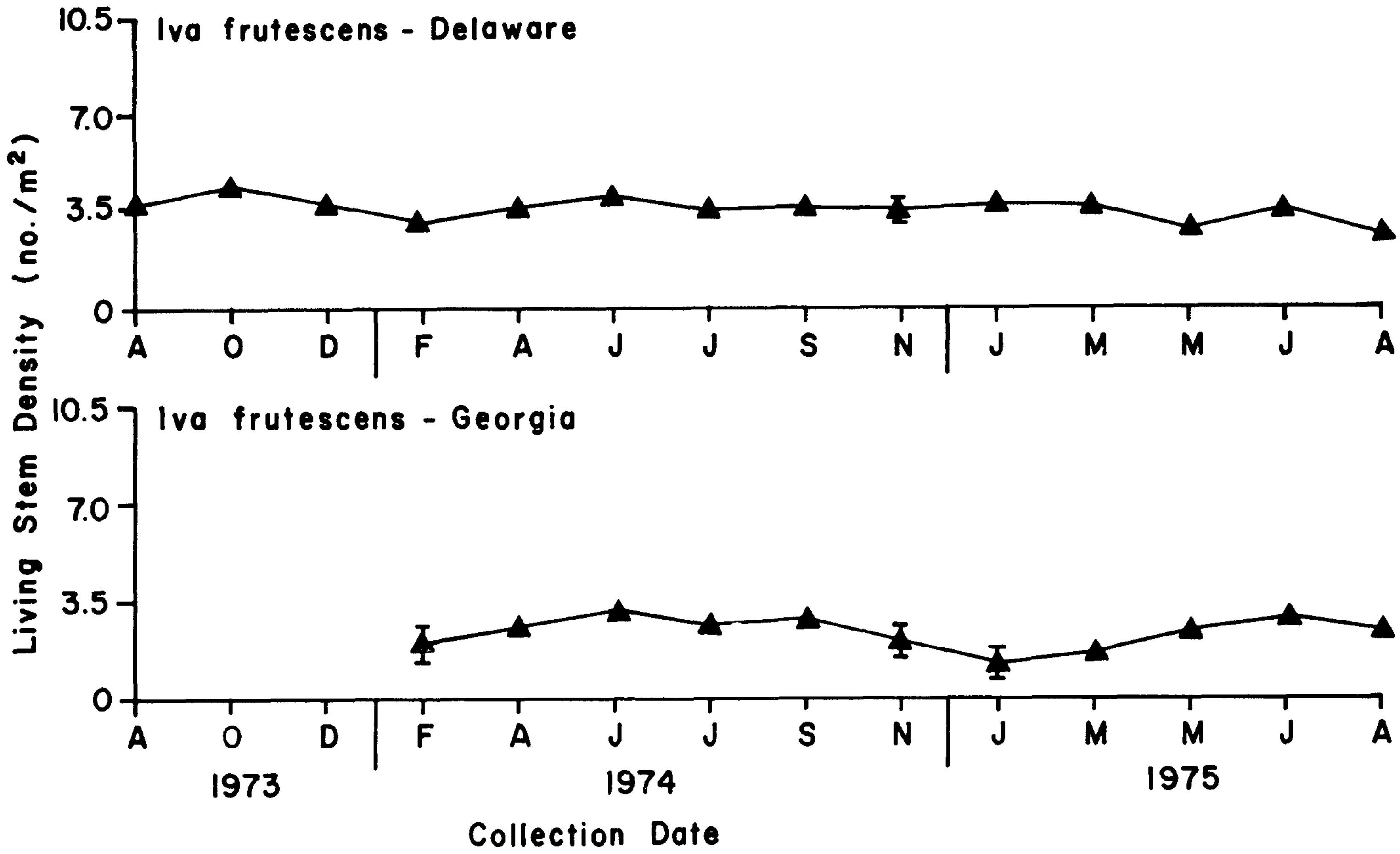


Figure 8. Natural logarithmic plots of living stem density (mean ± S.E.) for *Iva frutescens*. Standard errors are not shown when smaller than the size of the symbol.

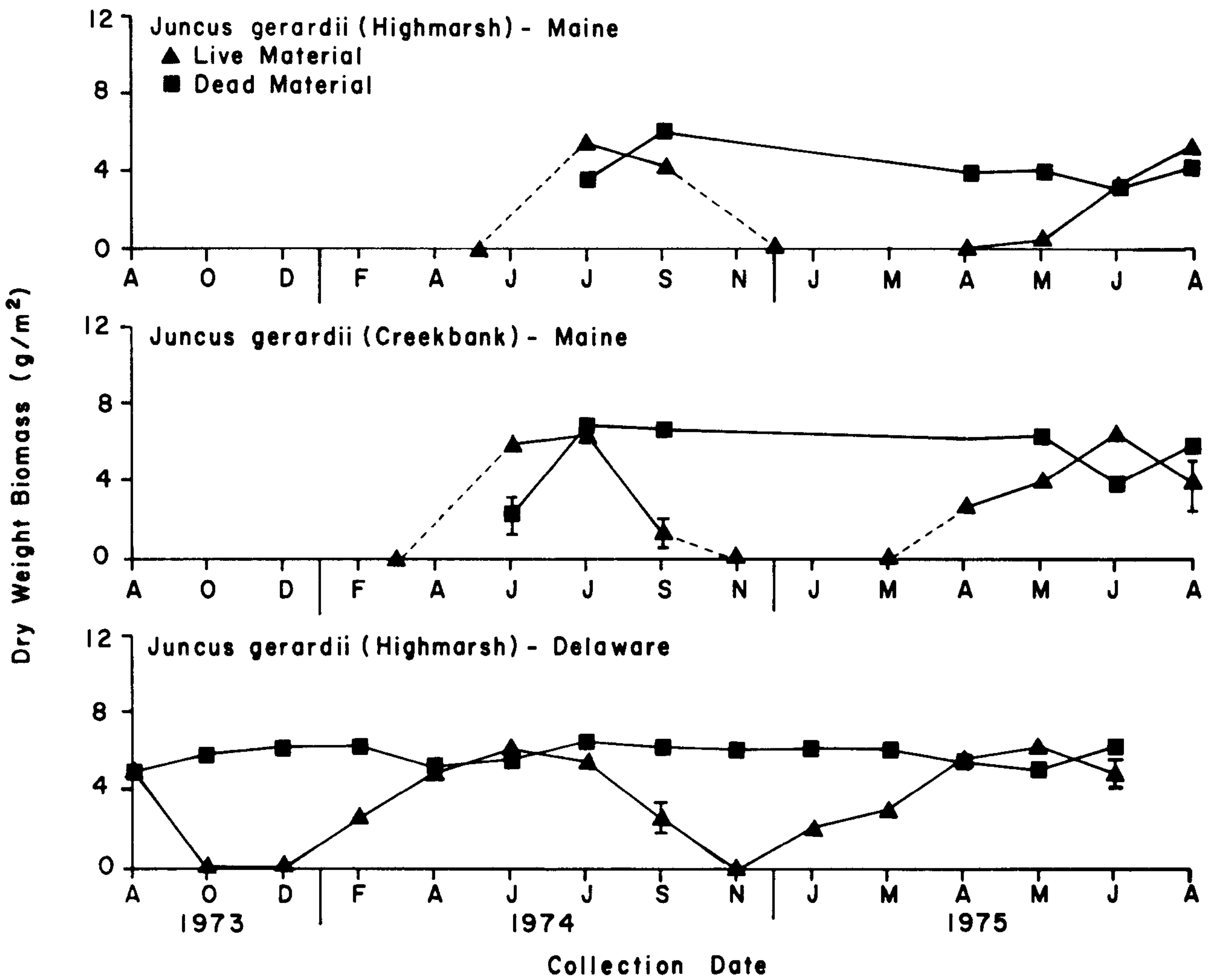


Figure 9. Natural logarithmic plots of living and dead aerial dry weight biomass (mean ± S.E.) for *Juncus gerardii*. Standard errors are not shown when smaller than the size of the symbol. Dashed lines represent projected values based on qualitative observations.

declined to zero in November where it remained during the winter months. This decline, indicated by a dashed line on Figure 9, was close to the actual conditions present based primarily on qualitative observations at the site and seasonal climatological data. In the highmarsh, the values of living biomass had a smaller range than that of the creekbank *Juncus gerardii*. The creekbank data indicated an earlier growth period possibly due to the buffering of environmental extremes by the tides. The highmarsh *Juncus gerardii* was subjected to greater climatological extremes early in the spring.

20. The dead *Juncus gerardii* biomass in Delaware (Figure 9) varied more than that of those plants previously discussed. Decline in dead biomass was evident in later spring concomitantly with increasing living biomass patterns. The increase in the Maine creekbank dead *Juncus gerardii* appeared to be directly associated with a rapid decrease in standing live biomass. The decreased dry weight of live material in the highmarsh sites, as compared to the creekbank site, was significant in determining the potential dead material contribution at any single sampling time. High values were indicative of late summer with minimum values consistently occurring in June or July at both Maine sites when conditions were appropriate for increased decomposition, increased direct tidal influence, and decreased death of living plants. The increased range of dead material present in the creekbank stand suggested increased tidal activity at this site. In few collections throughout the study did the living material exceed the dead plant material in any of the stands. The creekbank stand in Maine most closely approximated the Delaware highmarsh stand with respect to both living and dead material patterns.

21. Stem density data for *Juncus gerardii* (Figure 10) in Delaware showed an early growth initiation. The Maine data (Figure 10) also displayed a seasonal distribution with rapid early season growth in comparison to other marsh plants evaluated. The August peak in the Maine *Juncus gerardii* occurred considerably later in the season than the Delaware peak in May. In order to observe a clear growth pattern, the 7 April 1975 sample in the highmarsh Maine site was best repre-

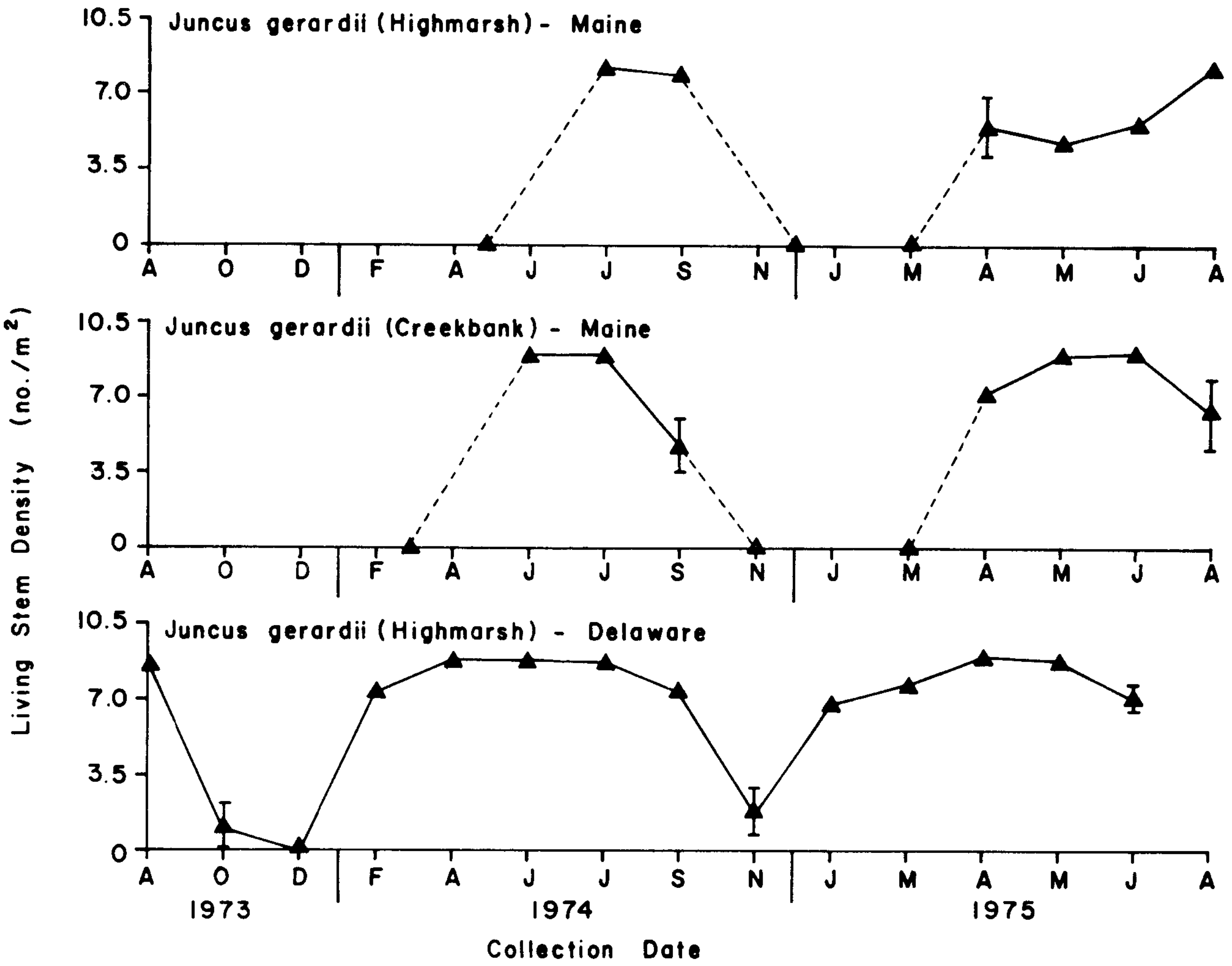


Figure 10. Natural logarithmic plots of living stem density (mean ± S.E.) for *Juncus gerardii*. Standard errors are not shown when smaller than the size of the symbol. Dashed lines represent projected values based on

sented by the value at the lower portion of the standard error bar (Figure 10). The Maine creekbank *Juncus gerardii* stand showed an earlier peak than the highmarsh stand. The seasonal pattern in Maine of the second sampling period from April to August of 1975 indicated the need for shorter sampling intervals in this area to assess the biomass and stem density changes. The 28-day interval from April to May appeared to be a more appropriate interval to detect the actual pattern of the density and living biomass components.

Phragmites communis and *Spartina cynosuroides*

22. *Phragmites communis* and *Spartina cynosuroides* (Figure 11) had similar living biomass patterns with broader seasonal ranges in *Spartina cynosuroides*. The lower biomass of *Spartina cynosuroides* found in the second year of study (13 January 1975) was missed or nonexistent during the bimonthly harvest in the first year of study. *Phragmites communis* and *Spartina cynosuroides* living biomass was lowest in winter and highest in late summer.

23. The August and October 1973 *Phragmites communis* samples were taken at a location that was apparently burned periodically by an unknown arsonist. Due to the threat of fire, the sampling site was relocated. The site relocation appeared to have little effect on the living biomass component; however, the dead component was significantly influenced since the first site had no litter accumulation while at the second site the litter was several inches deep. The living biomass was consistently higher than the dead in the *Spartina cynosuroides* plots where tidal influence was assumed to be more active. *Phragmites communis* had greater amounts of dead material (Figure 11) where the litter accumulation on the substrate surface was unmistakable.

24. Stem density values (Figure 12) displayed more seasonality in *Phragmites communis* than in *Spartina cynosuroides* stand since at no time during the study did the living stem density values decline to zero in *Spartina cynosuroides*. However, the ranges of living stem densities were quite similar. An earlier growth period was evident in the *Spartina cynosuroides* stand with maximum densities in late winter or early spring. Individual living stems weighed more in

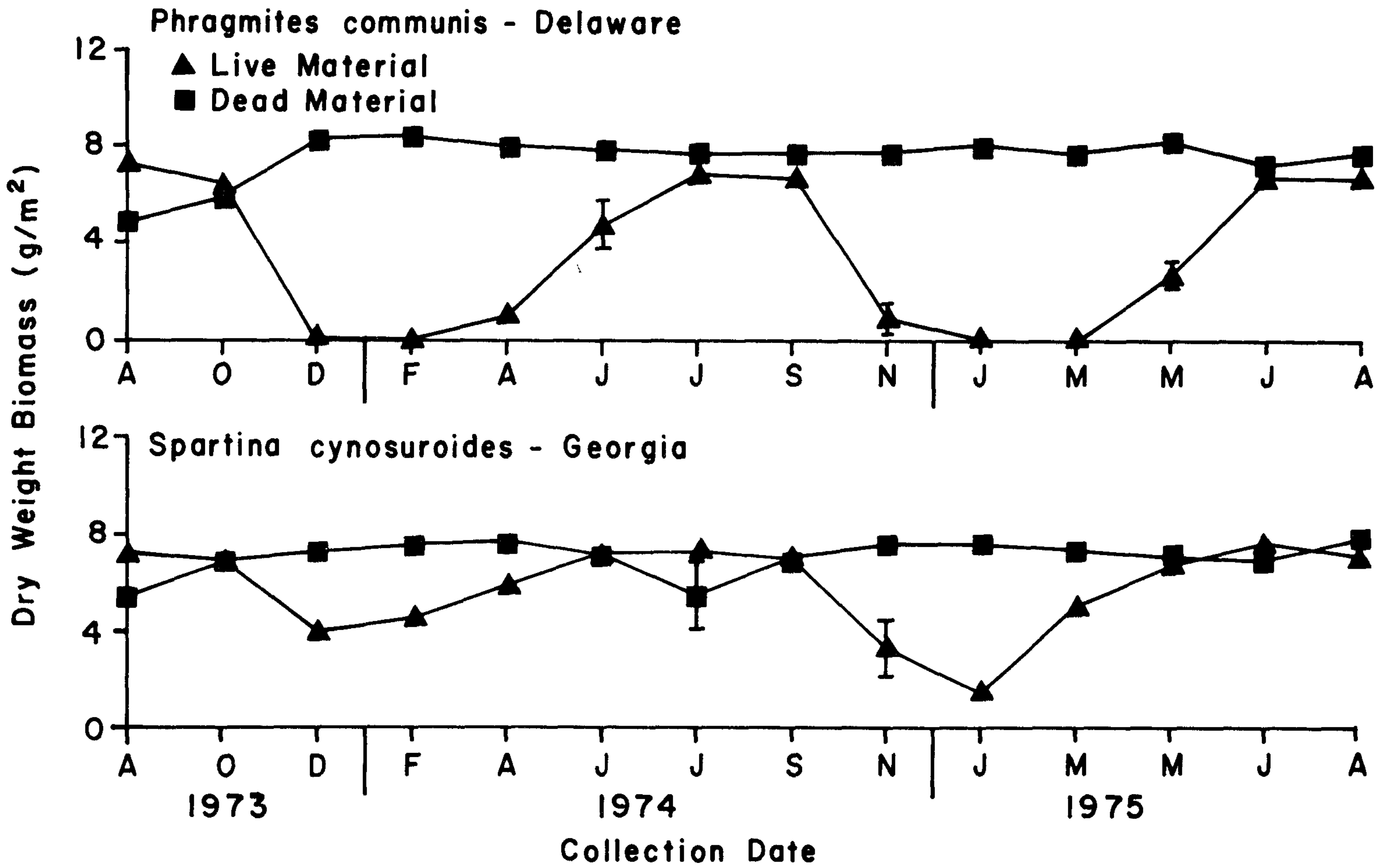


Figure 11. Natural logarithmic plots of living and dead aerial dry weight biomass (mean $\pm$ S.E.) for *Phragmites communis* and *Spartina cynosuroides*. Standard errors are not shown when smaller than the size of the symbol.

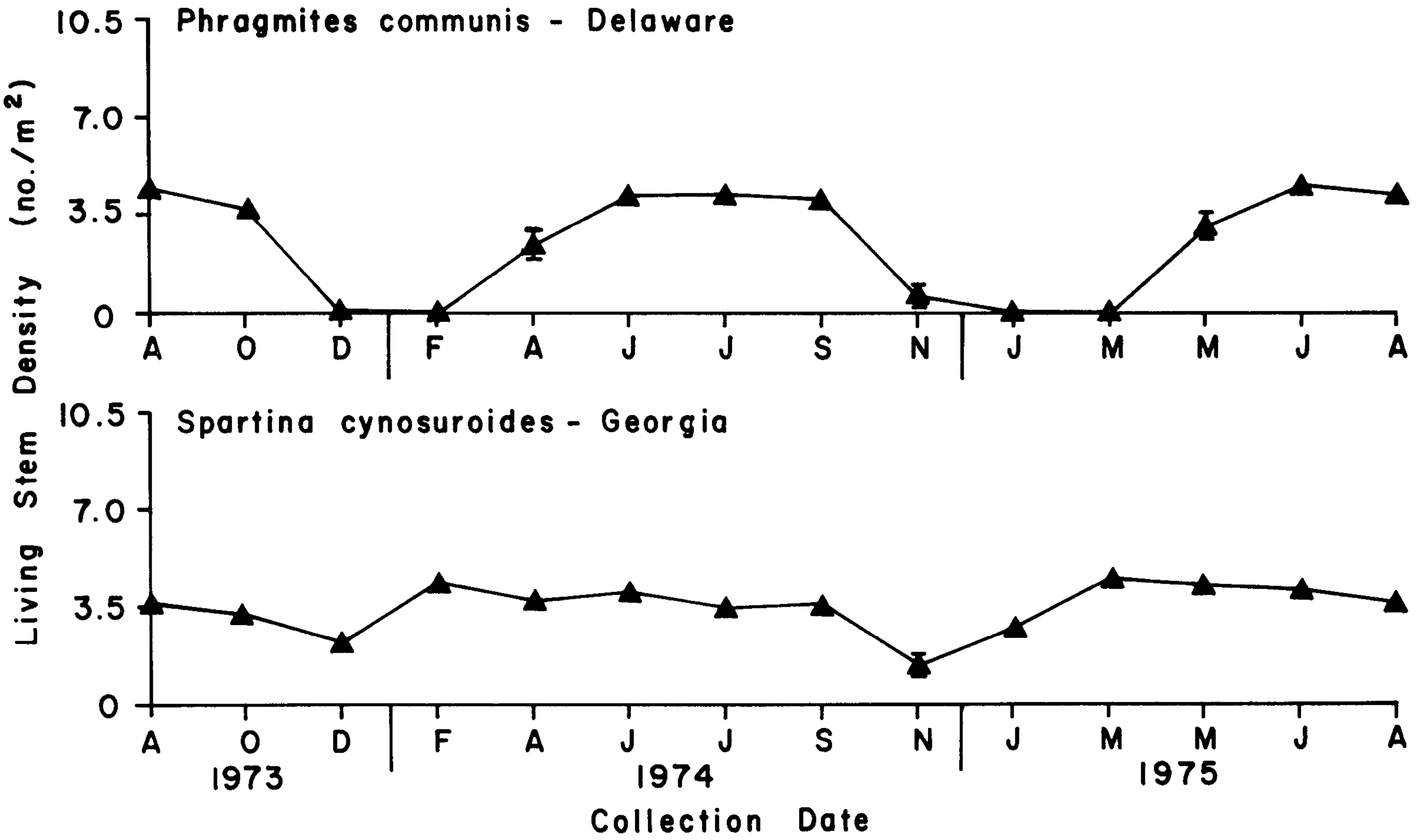


Figure 12. Natural logarithmic plots of living stem density for *Phragmites communis* and *Spartina cynosuroides*. Standard errors are not shown when smaller than the size of the symbol.

Spartina cynosuroides (Appendix C), which explains the increased live biomass observed in the *Spartina cynosuroides* stand when stem densities were similar.

Spartina alterniflora

25. Nearly identical patterns of live biomass were found in the two Maine sites (Figure 13). The range of living biomass in the highmarsh *Spartina alterniflora* was one-half that of the creekbank material as found in several other studies along the east coast (Reimold et al. 1973, Kirby and Gosselink 1976, Gallagher et al. In press). Unlike the *Juncus gerardii* data previously presented, the range of dead material (Figure 13) in both stands was very similar. The creekbank *Spartina alterniflora* had more instances where the live biomass exceeded the dead biomass when compared to the highmarsh stand, indicating increased tidal activity removing dead material. The highmarsh *Spartina alterniflora* had fewer dead portions on living stems, which also indicated that increased tidal activity removed these dead parts from the creekbank stand (Appendix C).

26. The live stem density data (Figure 14) resulted in nearly identical patterns at both sites, although the creekbank *Spartina alterniflora* density was higher than the highmarsh stem density. This condition was not indicative of the Georgia marshes where the stem density was greater in the highmarsh when compared to the creekbank (Gallagher et al. In press). Both maximum values were greater than comparative systems in Georgia. It was evident that the highmarsh plants had a slightly higher individual stem weight, also unlike that of the southeastern coastal systems (Appendix C). It must be noted that, based on tidal elevation data, the highmarsh stand was not one that was significantly higher in elevation (Part III). The increased dead removal potential resulted from the steep slope where the creekbank plants were found as opposed to a relatively flat area that was designated as highmarsh.

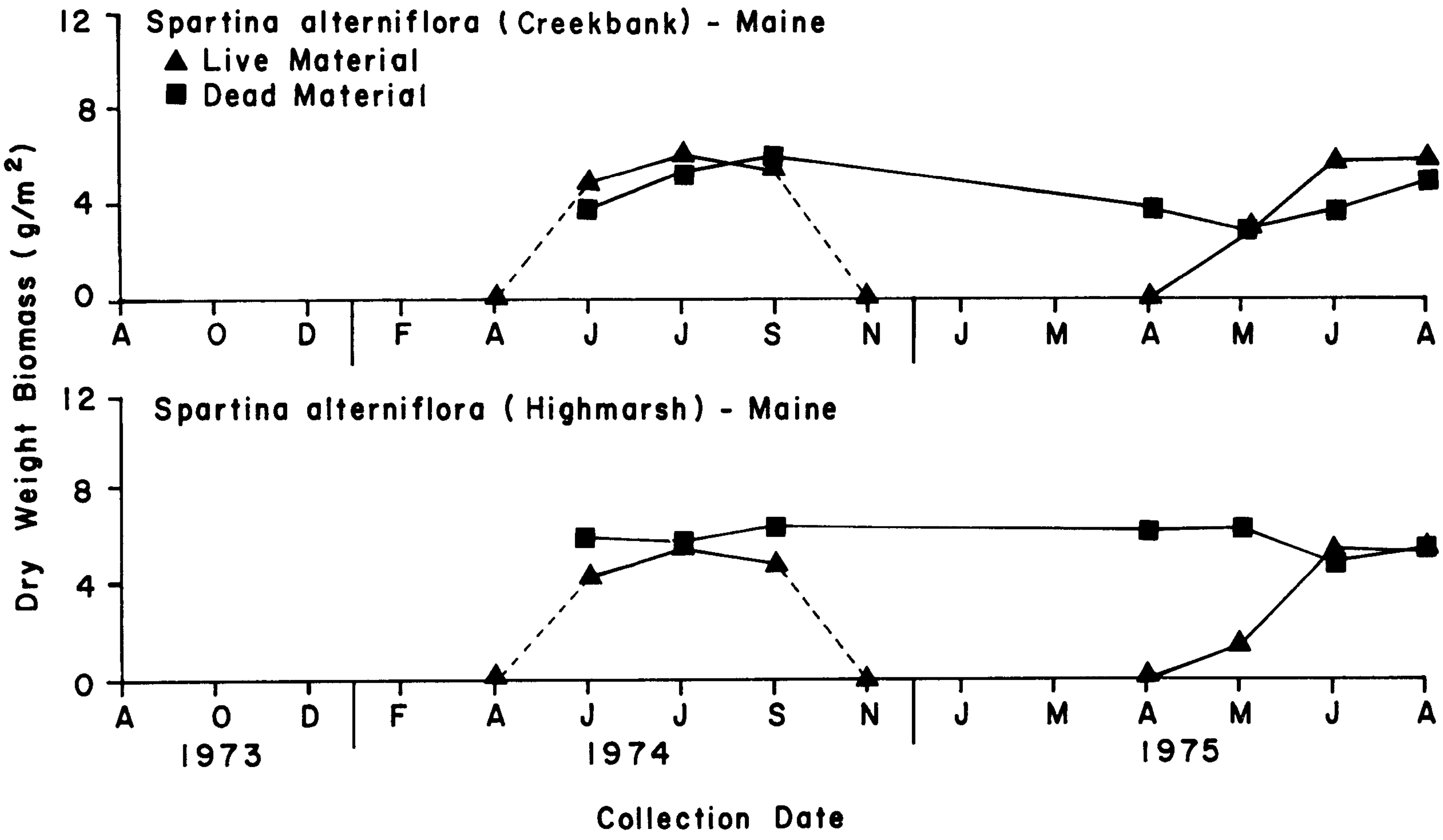


Figure 13. Natural logarithmic plots of living and dead aerial dry weight biomass (mean ± S.E.) for *Spartina alterniflora*. Standard errors are not shown when smaller than the size of the symbol. Dashed lines represent projected values based on qualitative observations.

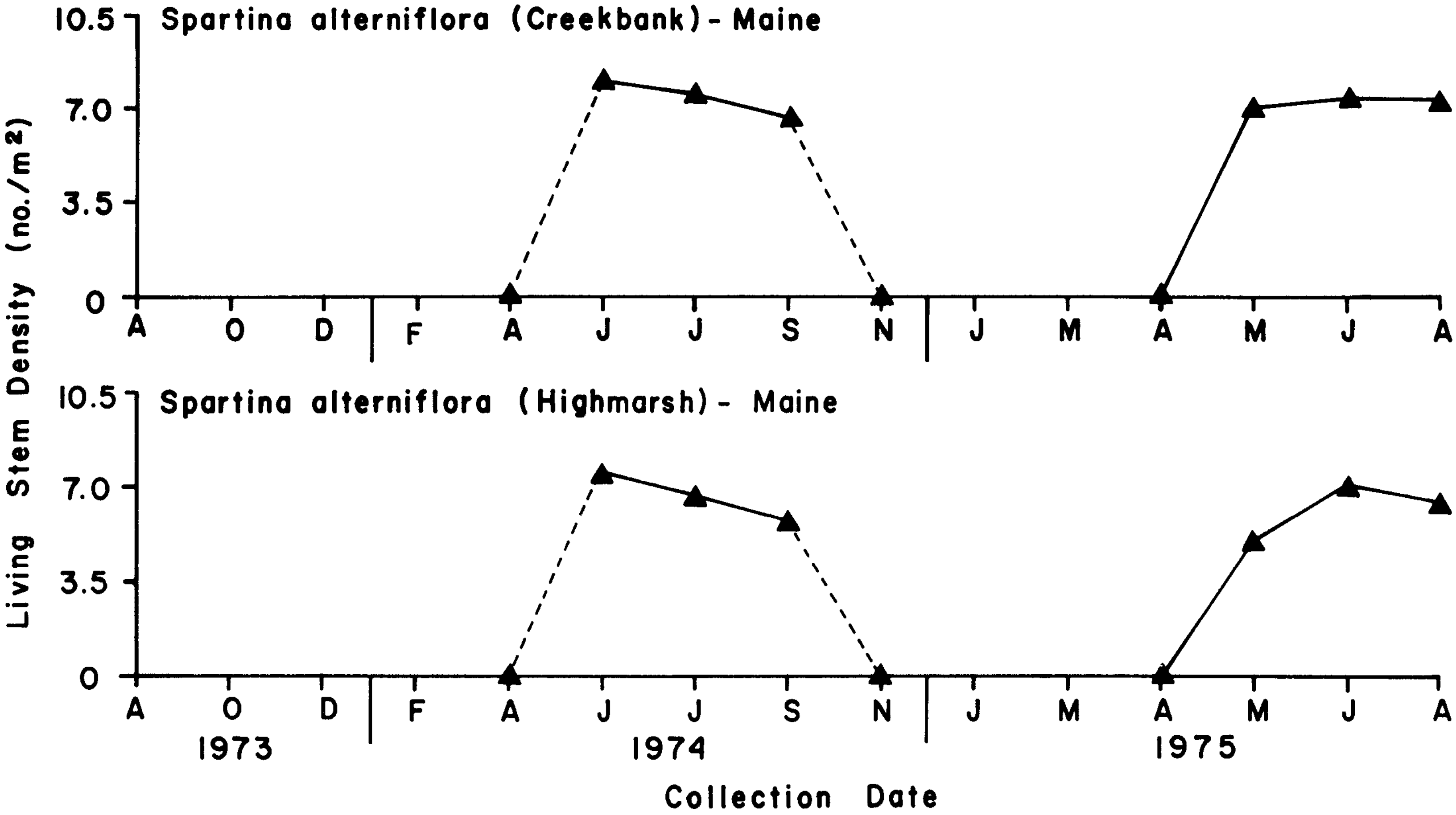


Figure 14. Natural logarithmic plots of living stem density (mean ± S.E.) for *Spartina alterniflora*. Standard errors are not shown when smaller than the size of the symbol. Dashed lines represent projected values based on qualitative observations.

Spartina patens

27. Living *Spartina patens* in the Delaware and Maine stands had a clearer pattern than that in the Georgia stand (Figure 15). However, the maximum standing crop of living biomass was nearly identical at all three locations. High living biomass of *Spartina patens* in Georgia was found in early spring of the first year and in summer of the second year. The dry weight of dead material (Figure 15) showed no evident seasonality but an extensive amplitude in the Georgia stand (Figure 15). The Maine and Delaware living *Spartina patens* was high in summer and low in winter. The Delaware *Spartina patens* dead biomass range was nearly one-half that of Georgia and more than one-third that of the Maine stand. The dead biomass in Maine was consistently lower during the second year of study. The increase in dead *Spartina patens* during the winter months in Maine was 487 g/m^2. This condition can be explained by the September sample assuming no disappearance of dead material during death of the 700.0 $\pm$ 99.87 g/m^2 of live material present at that time. This could have contributed another 700 g/m^2 to the dead component during the winter. Consequently, the decrease in dead material over the winter was estimated to be 213 g/m^2. An excessive litter mat was present in the Maine stand that introduced variability into the dead samples. The Delaware and Maine sites both showed a nearly constant excess of dead material when compared to the *Spartina patens* live biomass. These trends fluctuated frequently in the Georgia stand.

28. Live stem density values (Figure 16) showed a near constant amount of stems present in Georgia in comparison with the seasonal flux of values in the Maine and Delaware sites. The tufted growth form of *Spartina patens* was not visually obvious; however, this type of growth created variability in the Maine stem density data that ranged from a winter and early spring low of zero, to a variable maximum of 12880.0 $\pm$ 2438.3 $stems/m^2$ in August 1975. There was no statistical difference between this density and the previous 30 June 1975 sample where a stem density of 9520.0 $\pm$ 1430.5 $stems/m^2$ was recorded. The living stems of *Spartina patens* in Georgia were heavier than those of

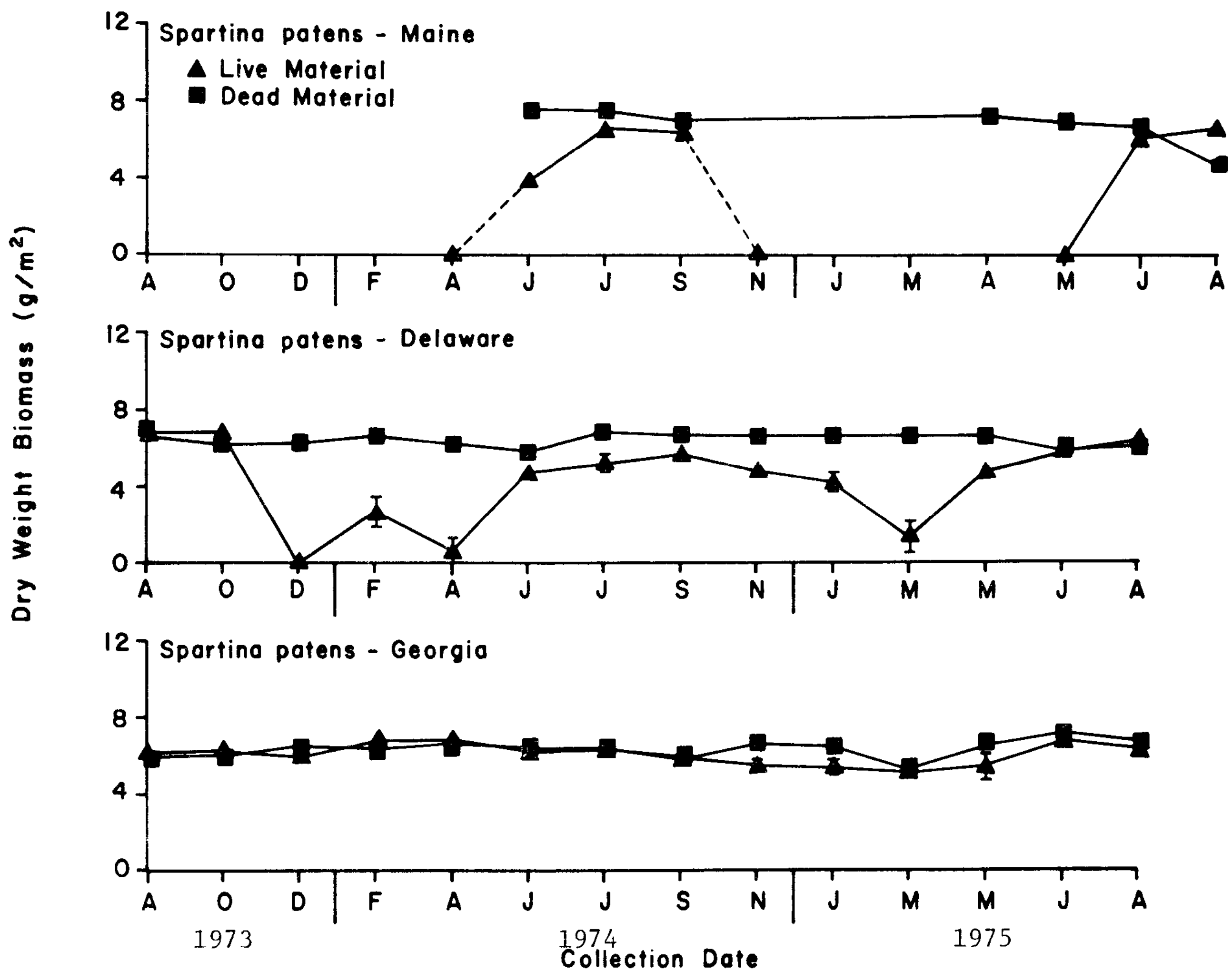


Figure 15. Natural logarithmic plots of living and dead aerial dry weight biomass (mean $\pm$ S.E.) for *Spartina patens*. Standard errors are not shown when smaller than the size of the symbol. Dashed lines represent projected values based on qualitative observations

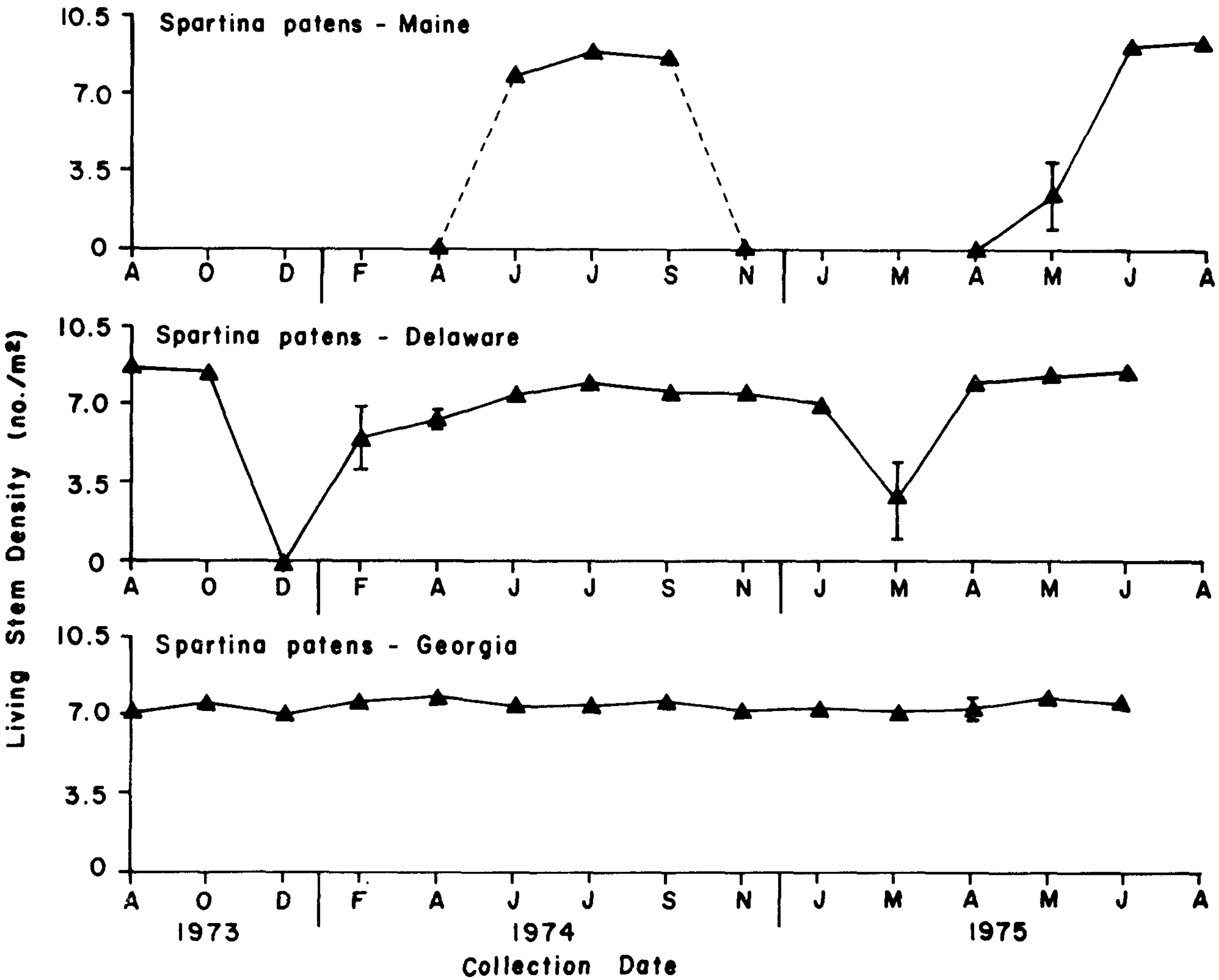


Figure 16. Natural logarithmic plots of living stem density (mean ± S.E.) for *Spartina patens*. Standard errors are not shown when smaller than the size of the symbol. Dashed lines represent projected values based on qualitative observations

the other sites, but the maximum density occurred in Maine (Appendix C). Therefore, it is difficult to assess which stand was influenced by better environmental conditions. Qualitative assessments of the sites would suggest that the Maine site had far better growing conditions.

Sporobolus virginicus

29. Biomass of living *Sporobolus virginicus* was at a maximum of 262.0 ± 45.9 g/m^2 on 24 September 1974, a value considerably lower than that of the other angiosperms evaluated (Figure 17). There was minor evidence of grazing by ungulates on *Sporobolus virginicus* so fences were constructed around the plots to act as exclosures. *Sporobolus virginicus* dead material decreased after the exclosures were constructed, but this decline was not directly attributed to the construction (Figure 17). The area was a transition zone between the forested highland and the regularly flooded marsh. Because of the transitional structure of this system, it may not be stable. Live stem densities exhibited a similar pattern to that in the Georgia *Distichlis spicata*, although density values were considerably higher than those of the *Distichlis spicata* plots (Figure 17). Variability was high in *Sporobolus virginicus*, which was attributed to its uneven distribution.

Living biomass

30. Latitudinal effects between similar and/or identical plant species are apparent in the living biomass minimum values summarized in Table 2. The Delaware and Maine angiosperms responded to the coldest winter temperature by producing no plants which grew or overwintered in a living state except for the woody *Iva frutescens* (Appendix A). The more distinct seasonal patterns of living biomass in Maine and Delaware appeared to be influenced by the number of days below 0° C (Appendix A). Maine had 142 days below freezing (October to April), while Georgia had only 3 days below freezing (December to March), on the average.

31. There was no evidence suggesting that difference in the length of the growing season had a pronounced effect on the maximum

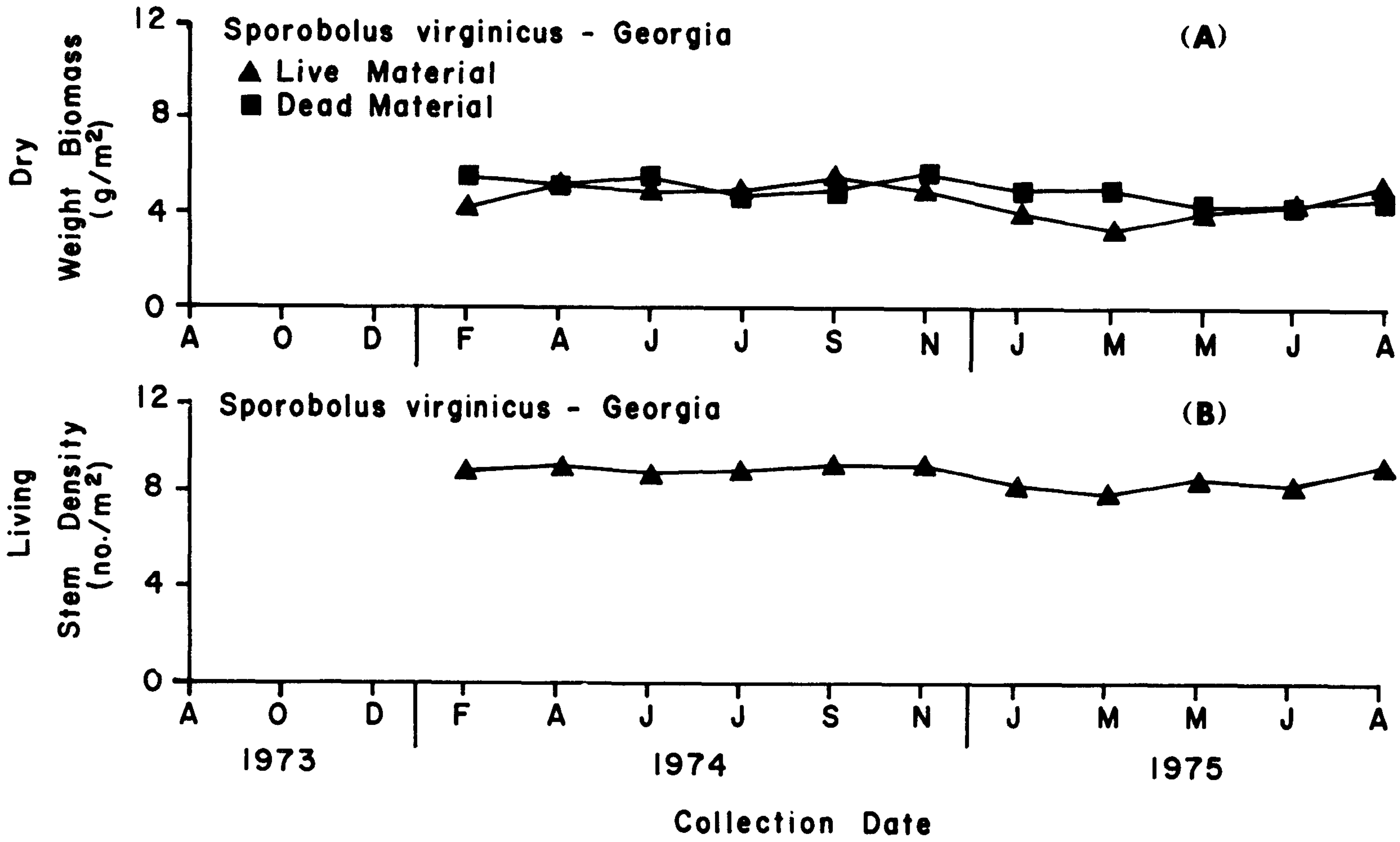


Figure 17. Natural logarithmic plots of living and dead dry weight biomass (mean ± S.E.) and living stem densities for *Sporobolus virginicus*. Standard errors are not shown when smaller than the size of the symbol

Table 2

Minimum and Maximum Values for Living Biomass, Dead Biomass, and Stem Densities by Species and Location

Location and species	Living biomass, g/m² Minimum	Living biomass, g/m² Maximum	Dead biomass, g/m² Minimum	Dead biomass, g/m² Maximum	Stem density, no./m² Minimum	Stem density, no./m² Maximum
MAINE						
J. gerardii (C)[a]	0 ± 0	644 ± 93	34 ± 19	1050 ± 197	0 ± 0	8680 ± 684
J. gerardii (H)[b]	0 ± 0	244 ± 56	22 ± 2	432 ± 34	0 ± 0	3880 ± 294
S. alterniflora (C)[a]	0 ± 0	431 ± 61	20 ± 6	432 ± 79	0 ± 0	3206 ± 664
S. alterniflora (H)[b]	0 ± 0	246 ± 23	187 ± 57	641 ± 49	0 ± 0	1804 ± 129
S. patens	0 ± 0	912 ± 196	132 ± 33	2124 ± 310	0 ± 0	12880 ± 2438
DELAWARE						
D. spicata	0 ± 0	1142 ± 348	248 ± 68	1302 ± 179	0 ± 0	6160 ± 630
I. frutescens	427 ± 117	1491 ± 380	107 ± 62	566 ± 216	18 ± 5	93 ± 25
J. gerardii	0 ± 0	560 ± 80	182 ± 33	748 ± 73	0 ± 0	8840 ± 930
P. communis	0 ± 0	1380 ± 150	1465 ± 125	4695 ± 601	0 ± 0	93 ± 8
S. patens	0 ± 0	962 ± 145	354 ± 52	962 ± 117	0 ± 0	5900 ± 574
GEORGIA						
B. frutescens	648 ± 15	1860 ± 122	184 ± 14	291 ± 36	213 ± 12	380 ± 27
D. spicata	128 ± 12	458 ± 92	331 ± 64	1260 ± 285	942 ± 87	2300 ± 700
I. frutescens	116 ± 56	1288 ± 365	538 ± 56	1396 ± 307	5 ± 2	25 ± 3
S. cynosuroides	4 ± 1	2177 ± 204	292 ± 99	2584 ± 340	4 ± 2	92 ± 13
S. patens	176 ± 37	980 ± 190	236 ± 72	1324 ± 161	1266 ± 148	2900 ± 484
S. virginicus	39 ± 14	262 ± 46	80 ± 14	316 ± 21	1420 ± 334	4360 ± 872

[a]Creekbank.

[b]Highmarsh.

values. One might assume that the substrate properties alone could be the dominating factor in regulating the maximum live biomass. The optimum growth habitat is not known for many of these minor marsh plants, which also makes latitudinal comparisons inconclusive.

Dead biomass

32. Dead biomass maximum and minimum values summarized in Table 2 reflect the influence of the tides and the rate of decomposition. The most variation between maximum and minimum dead biomass was found in the Maine stands. These plants were all found to be growing below mean high water (mhw), indicating a more frequent tidal flushing (Part III). The Delaware and Georgia sites had similar percent variation between maximum and minimum dead biomass. Based on mhw data (Part III), the variation of dead material should be similar in Delaware and Georgia as indicated by the results. Due to the extreme difference in climate, decomposition should be greater in Georgia. *Spartina patens* data support this conclusion, although the variability of the tides is enough to suggest that it is a predominating influence in determining the amount of dead material that remains in any single stand.

33. The amount of dead material present may be extremely important as a nutrient source for continued production (Maye 1972). In addition, the living contribution is the material that dies and can greatly vary between sites. Therefore, quantification of mortality is important in determining an accurate assessment of the system.

Tidal influence

34. The tidal influence is an important entity that strongly influences the growth of the plants and has been called "tidal subsidy" by Odum (1961) and Odum and Riedeburg (1976). They suggested that those plants influenced regularly by the tides, particularly the tall height form of *Spartina alterniflora*, have a greater growth potential based on increased nutrient loads, aeration, and a number of other environmental factors regulated by tidal activity. The increased stem densities of the Maine plants compared with the Delaware and Georgia

plants (Table 2) support this theory. When comparing the creekbank and highmarsh stands in Maine, the maximum living biomass also supports this hypothesis, although the creekbank *Spartina alterniflora* values might vary according to where the highest percentage of samples were taken (i.e., above or below mhw). In comparing maximum living biomass between states, there is no evidence to support the tidal subsidy theory, and the site differences, excluding tidal influence, may have been great enough to dictate the results obtained. Hubbard (1969) suggested that the length of inundation alone can influence plant response.

35. Because the climatic differences, soil properties, tidal activity, and other biotic and abiotic factors are acting on any single site, the collective action might be termed environmental metabolism. This collective term would then indicate not simply the entities which together form the environment, but the activity and interaction of these entities. The components which quantify environmental metabolism must be examined for each site to draw conclusions related to growth response.

Seasonal patterns

36. The resulting seasonal patterns obtained in this study were similar to those obtained by Wiegert and McGinnis (1975) in three South Carolina old fields. Live biomass of several angiosperms (e.g., the Georgia *S. patens*, *D. spicata*, and *S. virginicus*) did not demonstrate clear seasonality of all components studied because of the longer growth period. The raw data do, however, suggest seasonality in most components (Appendix C). A cyclic seasonal pattern of the nature obtained indicates the stability of the stand (Wiegert and McGinnis 1975).

Sampling problems

37. In sampling the angiosperms, numerous difficulties arose that should be noted. On 17 December 1973, the living *Distichlis spicata* in Delaware was zero; however, the live stem density for the same month was 700.0 ± 94.9 stems/m^2. It should be noted that a

majority of the living stems harvested consisted mainly of dead portions (99.0 percent). The stripping of the dead material from the living tissue resulted in sample biomass too small for accurate weighing. Therefore, the expansion of the data to a square metre basis increased the mean number of stems by 100 without an increase in the live biomass that could not be determined.

38. *Juncus gerardii* in Delaware presented similar errors. Although inadequate amounts from biomass determination were found, the living shoots of *Juncus gerardii* had a high density in early spring. The response of *Juncus gerardii* was such that it is a cool season plant, with early shoot growth during a period when air temperatures were still periodically below freezing. An increase in dead biomass early in the season in this species was possibly due to high mortality of the young shoots during freezes. For whatever reason(s), densities of small young shoots were extremely high, but living biomass increases could not be detected.

39. Both the *Distichlis spicata* and *Juncus gerardii* discrepancies were a direct result of inadequate sample size. Minimum sample sizes determined in August were inadequate when utilized during the winter months.

Research needs

40. Although this study might provide additional data for those working in marsh systems, additional information on the physiological tolerances and the importance of these plants to the total system is still needed. Because of the limited areal extent of these plants, they have been neglected in marsh ecosystem studies. If it is the purpose of the marsh ecologist to describe, quantify, and model these systems, the minor marsh plants must be examined more fully. The productivity of these plants must also be examined in more detail.

41. The baseline information provided in this portion of the study indicates that production cannot be determined solely by biomass information. However, tidal activity, decomposition rates, and mortality, essential components of the salt marsh-estuarine system, must be

quantified and assessed with respect to biomass data. This consideration is examined in Part III.

LITERATURE CITED IN PART II

Cooper, A. W. 1969. Salt marshes. In Odum, H. T., B. J. Copeland, and E. A. McMahan, ed. Coastal Ecological Systems of the U. S. Vol. I. Report to the Water Pollution Control Administration. The Conservation Foundation. Washington, D. C.

Day, J. W., W. G. Smith, P. R. Wanger, and W. G. Stowe. 1973. Community structure and carbon budget of a salt marsh and shallow bay estuarine system in Louisiana. Louisiana State University, Publication No. LSU-SG-72-04, Baton Rouge. 79 p.

de la Cruz, A. A. 1973. The role of tidal marshes in the productivity of coastal waters. ASB Bull. 29(4): 147-156.

Durand, J. B. and R. J. Nadeau. 1972. Water resources in the Mullica River Basin. Part I. Biological evaluation of Mullica River. Great Bay Estuary. New Jersey Water Resources Research Institute, Rutgers Univ., New Brunswick. 138 p.

Gallagher, J. L., R. J. Reimold, R. A. Linthurst, and W. J. Pfeiffer. In press. Aerial production, mortality, and mineral accumulation dynamics in *Spartina alterniflora* and *Juncus roemerianus* in a Georgia salt marsh. (Ecology).

Good, R. E. 1965. Salt marsh vegetation, Cape May, New Jersey. Bull. New Jersey Acad. Sci. 10: 1-11.

Gosselink, J. G., E. P. Odum, and R. M. Pope. 1974. The value of the tidal marsh. LSU-SG-74-03. Center for Wetland Resources, Louisiana State University., Baton Rouge, La., 39 p.

Hatcher, B. G. and K. H. Mann. 1975. Aboveground production of marsh cordgrass (*Spartina alterniflora*) near the northern end of its range. J. Fish. Res. Bd. Can. 32: 83-87.

Hubbard, J. C. E. 1969. Light in relation to tidal immersion and the growth of *Spartina townsendii* (s.l.). J. Ecol. 57: 795-804.

Johnson, M. 1970. Preliminary report on species composition, chemical composition, biomass, and production of marsh vegetation in the upper Patuxent Estuary, Maryland. Chesapeake Biol. Lab. Ref. No. 70-130: 165-178.

Keefe, C.W. and W. R. Boynton. 1973. Standing crop of salt marshes surrounding Chincoteague Bay, Maryland - Virginia. Chesapeake Sci. 14: 117-123.

Kirby, C. J., Jr. 1971. The annual net primary production and decomposition of salt marsh grass *Spartina alterniflora* Loisel. in the Barataria Bay estuary of Louisiana. Ph.D. Thesis, Louisiana State University, Baton Rouge. 74 p.

Kirby C. J. and J. G. Gosselink. 1976. Primary production in a Louisiana gulf coast *Spartina alterniflora* marsh. Ecology 57: 1052-1059.

Maye, P. R., III. 1972. Some important inorganic nitrogen and phosphorus species in Georgia salt marsh. Environmental Resources Center, Georgia Inst. of Tech. Rept. 0272, 60 p.

Mendelssohn, I. A. and K. L. Marcellus. 1976. Angiosperm production of three Virginia marshes in various salinity and soil nutrient regimes. Chesapeake Sci. 17:15-23.

Morgan, M. H. 1961. Angiosperm production on a salt marsh. M. S. thesis, University of Delaware, Newark. 34 p.

Odum, E. P. 1961. The role of tidal marshes in estuarine production. The N. Y. State Conserv. 15:12-15.

Odum, E. P. and A. A. de la Cruz. 1967. Particulate organic detritus in a Georgia salt marsh estuarine ecosystem. pp. 383-388. In Estuaries, G. H. Lauff (ed.). Publ. AAAS No. 83, Washington, D.C.

Odum, E. P. and C. H. Riedeburg. 1976. A dye study of interstitial water flow in tidal marsh sediments. In: Abstracts of papers submitted for the 39th Annual Meeting ASLO, Skidaway Institute of Oceanography, Savannah, Ga.

Pomeroy, L. R., L. R. Shenton, R. D. H. Jones, and R. J. Reimold. 1972. Nutrient flux in estuaries, pp. 275-293. In: G. E. Likens (ed.), Nutrients and Eutrophication. Vol. I., Am. Soc. Limnol. Oceanogr.

Reimold, R. J. 1974. Mathematical modeling - *Spartina*, pp. 393-406. In: R. J. Reimold and W. H. Queen (eds.). Ecology of Halophytes. Academic Press, Inc., N. Y.

Reimold, R. J. 1976. Mangals and salt marshes of eastern United States, pp. 157-164. In: V. J. Chapman (ed.) Wet Coastal Ecosystems. Elsiver Scientific Publ. Co., Amsterdam.

Reimold, R. J., J. L. Gallagher, and D. E. Thompson. 1973. Remote sensing of tidal marsh. Photogram. Eng. Vol. 39(5):477-488.

Reimold, R. J., J. L. Gallagher, R. A. Linthurst, and W. J. Pfeiffer. 1975. Detritus production in coastal Georgia salt marshes, pp. 217-228. In: E. Cronin (ed.). Estuarine Research. Vol II. Academic Press, Inc., New York.

Smalley, A. E. 1958. The role of two invertebrate populations, *Littorina irrorata* and *Orchelimum fidicinum* in the energy flow of a salt marsh ecosystem. Ph.D. thesis, University of Georgia, Athens. 126 p.

Snedecor, G. W. and W. G. Cochran. 1967. Statistical Methods. The Iowa State University Press, Ames, Iowa. 593 p.

Stroud, L. M. and A. W. Cooper. 1968. Color-infrared aerial photographic interpretation and net primary productivity of a regularly flooded North Carolina salt marsh. Water Resources Research Inst. Report No. 14, North Carolina State University at Raleigh. 86 p.

Sweet, D. C. 1971. The economic and social importance of estuaries. Environ. Prot. Agency. Water Quality Office. Washington, D. C. pp 33-49.

Teal, J. M. 1962. Energy flow in the salt marsh ecosystem of Georgia. Ecology 43: 614-624.

Wiegert, R. G. 1962. The selection of an optimum quadrat size for sampling the standing crop of grasses and forbs. Ecology 43: 125-129.

Wiegert, R. G. and F. C. Evans. 1964. Primary production and the disappearance of dead vegetation in an old field. Ecology 45: 49-63.

Wiegert, R. G. and J. T. McGinnis. 1975. Annual production and disappearance of detritus on three South Carolina old fields. Ecology 56: 129-140.

Wiegert, R. G., R. R. Christian, J. L. Gallagher, J. R. Hall, R. D. H. Jones, and R. L. Wetzel. 1975. A preliminary ecosystem model of coastal Georgia *Spartina* marsh. pp. 583-601. In: L. E. Cronin (ed.). Estuarine Research. Academic Press, Inc., New York.

PART III: AN EVALUATION OF DETRITUS FLUX, ESTIMATED NET AERIAL PRIMARY PRODUCTIVITY, AND MORTALITY OF SELECTED ESTUARINE ANGIOSPERMS IN MAINE, DELAWARE, AND GEORGIA

Introduction

42. Ecological studies of salt marsh systems along the east coast of the United States are prominent in the literature (Wentz et al. 1974). Common to even the earliest studies of salt marsh vegetation and distribution is the discussion related to the importance of the tides (Ganong 1903, Harshberger 1911, Johnson and York 1915, Conrad 1935, Penfound and Hathaway 1938, Taylor 1938, Chapman 1940, Miller and Egler 1950, Jackson 1952, Kurz and Wagner 1957, Chapman 1974, Adams 1963, Blum 1968). The role of these tidally influenced wetlands is documented (Davis 1910, Daigh et al. 1938, Odum 1961, de la Cruz 1965, Redfield 1965, Waits 1967, Udell et al. 1969, Redfield 1972, de la Cruz 1973), and the various processes that contribute to the biological productivity are used to estimate the metabolic activity of the salt marsh plant species because of their importance in system energetics studies (Smalley 1958, Odum 1961, Schelske and Odum 1961, Morgan 1961, Teal 1962, Good 1965, Stroud and Cooper 1968, Johnson 1970, Kirby 1971). A variety of methods have been employed to make such an estimate of productivity (Kirby 1971, Singh et al. 1975); however, most studies are limited to the primary plants whose areal extent dominates the southeastern coastal marshes (i.e., *Spartina alterniflora* and *Juncus roemerianus*). Works by Keefe (1972), de la Cruz (1973), and Hatcher and Mann (1975) summarized these estimates.

43. In an attempt to assess production of salt marsh plants, studies related to the importance of tidal activity have been initiated to acquire more accurate estimates of net primary production and detritus flux (Smalley 1958, Kirby 1971, Gallagher and Reimold 1973, and Reimold et al. 1975). The importance of detritus in the coastal waters is well documented (Clark 1946, Jannasch and Jones 1959,

Riley 1963, Odum and de la Cruz 1963, 1967, Darnell 1967, Heald 1969). One method of estimated net aerial primary production was developed for grassland systems (Wiegert 1962, Wiegert and Evans 1964) which tended to increase earlier estimates because it considered disappearance of dead material between harvest intervals (Wiegert et al. 1975, Reimold et al. 1975, Bradbury and Hofstra 1976, Gallagher et al. In press).

44. The purpose of this study was to utilize and evaluate this method in the salt marsh in relation to those plant species considered as minor, based on areal extent, as did Reimold et al. (1975) and Gallagher et al. (In press) on major salt marsh plants. The study was designed to contribute additional information on estuarine tidal subsidy related to net primary production of minor marsh plants. The results will be useful in studies of energetics and photosynthetic response of the selected minor marsh plant species over a broad latitudinal range. Detritus flux, net aerial primary productivity, and mortality of living plants are also evaluated. These results provide a means of value comparison of several ecological attitudes of the plants studied and should be used for management decisions regarding dredged material disposal.

Methods

Site selection

45. Saline marsh sites in Maine, Delaware, and Georgia were selected for study (Figures 1 - 3). Selection criteria included a broad latitudinal range (31°19' to 44°34'), logistically feasible access within the time allowed for collection and preparation of samples (1 week), and laboratory facilities which could be utilized for immediate preparation of the samples. Marshes were selected which had similar vegetative diversity with monospecific stands of the plant species to be evaluated. Subjectively chosen sites were preferred in order to limit the effect of varying environmental conditions.

Quadrat size

46. Optimum quadrat size used for sampling aerial plant material was determined in August 1973 according to the method of Wiegert (1962). The plant species chosen for investigation, the states where they were sampled, and the quadrat sizes used are shown in Table 3.

Plant species

47. *Juncus gerardii* stands in Maine were referred to as creekbank where the plants were growing on a steep slope above the *Spartina alterniflora* and as highmarsh where the plants were growing on a relatively flat site landward on the creekbank plants. Similar differentiation was employed in the *Spartina alterniflora* stands. The *Juncus gerardii* stands in Maine were mixed with another rush nearly identical in growth form, *Juncus balticus*. Because of the periodic absence of fruiting or flowering structures necessary for separating the two during sampling, this stand was treated as a monospecific stand of *Juncus gerardii*.

48. A majority of the plant species sampled had a limited range of growth and were therefore unavailable for sampling in all states. *Phragmites communis* and *Spartina cynosuroides* had a broader latitudinal growth range than sampled; however, they were not found in an area where sampling could be done based on the criteria discussed earlier. Finally, *Spartina alterniflora* was found in all locations but sampled only in Maine. Production estimates for *Spartina alterniflora* in the southeastern and middle Atlantic coastal regions were already well documented in the literature (de la Cruz 1973, Hatcher and Mann 1975, Mendelssohn and Marcellus 1976, Reimold et al. 1975, and Gallagher et al. In press). Therefore, this angiosperm was investigated only in Maine where literature values were unavailable.

Harvest methods

49. Contiguous paired plots as described by Wiegert and Evans (1964) were employed for the collection of the aerial plant material

Table 3

Angiosperms Evaluated, Their Geographic Location, and Sample Quadrat Size for Collection Sites Evaluated

Angiosperms	Location[a]			Quadrat size m^2
Distichlis spicata		D	G	0.01
Juncus gerardii[b]	M			0.01
Juncus gerardii[c]	M	D		0.01
Phragmites communis		D		0.50
Spartina alterniflora[b]	M			0.10
Spartina alterniflora[c]	M			0.10
Spartina cynosuroides			G	0.50
Spartina patens	M	D	G	0.01
Sporobolus virginicus			G	0.01

[a]M = Maine; D = Delaware; G = Georgia

[b]Creekbank.

[c]Highmarsh.

and litter. Stainless steel hand pruners or dissecting scissors were utilized for harvesting. Dissecting scissors were used on all plots of 0.1 m^2 or smaller to increase the accuracy of the harvest by potentially decreasing experimental error in these small quadrats.

50. Five samples were taken simultaneously within each stand, at all locations, and at 56-day intervals from the initiation of the study on 27 August 1973 through its termination on 25 August 1975 in Delaware and Georgia. *Sporobolus virginicus* sampling was initiated in February 1975 in Georgia. Maine sampling was not initiated until 3 June 1974 and continued until the termination of sampling at the other locations. However, because of the severity of the winter and the impossibility of accurate sampling during months when the Maine site was covered with ice and snow, sampling in Maine was restricted to late spring, summer, and early fall. In addition, one 28-day sampling interval was necessary to approximate initiation time of spring plant growth in Maine.

51. Plant material harvested in the field was separated into live and dead components and placed in polyethylene bags of sizes ranging from 0.9 ℓ to 208.0 ℓ dependent upon the amount of material present. Evidence of green material on the stem dictated the selection of living plants, and material with an absence of green coloration was assessed to be dead. The samples were returned to the preparation laboratory at the respective sites immediately following the field sampling. Here they were weighed using a Model 2197 Ohaus 5-kg balance with a sensitivity of $\pm$ 0.5 g to determine fresh weight values to the nearest 1.0 g. Dead portions of the living plants were stripped off and weighed separately. The necessity of subsampling to evaluate dry weights was determined based upon the amount of material which would adequately fill a 0.9-ℓ jar. Samples harvested in Delaware and Maine were packaged and transported by air to Georgia where they were placed in jars and dried in a mechanically convected forced draft oven at 100° C to a constant weight. All samples were removed from the oven when dry and weighed on a Mettler Model P11, 11-kg-capacity

balance with a sensitivity of $\pm$ 0.05 g. Subsample data were expanded to include the complete harvest fresh weights, and subsequently all data were expanded to a square metre basis.

Instantaneous detritus flux rates

52. Instantaneous detritus flux rates were calculated from paired plots (Wiegert and Evans 1964, Reimold et al. 1975, Gallagher et al. In press) using Equation 1:

$$r_i = \frac{\ln (w_0/w_1)}{t_1 - t_0} \quad (1)$$

where: r_i = detritus flux, g/g/day

w_0 = dry weight of dead material at time t_0, days

w_1 = dry weight of dead material at time t_1, days

53. Equation 1 is based on the assumptions that the biomass of the two paired quadrats was identical and that the rate of detritus flux of the two quadrats was equal. The addition of a tidal parameter, not found in an old field, caused a rejection of a third assumption made by Wiegert and Evans (1964) (i.e., no additional material could be added to the dead material of the second quadrat during the harvest interval). This new environmental parameter, experienced by Reimold et al. (1975) and Gallagher et al. (In press), but not by Wiegert and Evans (1964), permitted both addition of material to the second quadrat "dead plots" as well as total removal of dead material from the plot, thus the term "detritus flux," as opposed to Wiegert and Evans' (1964) "disappearance of dead material."

54. In order for Equation 1 to work efficiently, it was necessary for w_0 and w_1 to be nonzero values. Therefore, the value of 1 g/m^2 was added to all dead component biomass values. This procedure allowed computation of rates where w_1 was zero (representing 100 percent disappearance) as well as where w_0 was zero (indicating a contribution to the plot). Rates were computed based on five observations for each interval in each monospecific plant stand. All statistical computations

were conducted according to the method outlined by Snedecor and Cochran (1967) and were based on dry weight biomass information.

Detritus flux

55. The resultant values were utilized to compute detritus flux per interval (X_i) using Equation 2:

$$X_i = [(a_i + a_{i-1})/2] \, r_i t_i \tag{2}$$

where:
a_i = standing crop of dead material, g/m^2
a_{i-1} = standing crop of dead material at the second harvest, g/m^2
r_i = instantaneous rate of detritus flux during the interval
t_i = time interval, days

Annual detritus production was computed by summing monthly values and adjusting to obtain a yearly estimate.

Primary production and mortality

56. Estimated net aerial primary production and mortality were computed according to the procedures outlined by Wiegert and Evans (1964) and Gallagher et al. (In press). Mortality was computed as the change in dead biomass (Δa) plus the amount of material that disappeared during the harvest period. Net aerial primary production was then calculated as the change in living biomass (Δb) during the harvest interval plus the concomitant mortality value. In addition, it had been suggested by Wiegert and McGinnis (1975) and Gallagher et al. (In press) that the instantaneous detritus flux rates be averaged for the study period and utilized for computations of net aerial primary production. Both methods were utilized and are discussed later.

57. The difficulty encountered in Maine relative to sampling consistently at 56-day intervals resulted in utilizing only the average of the detritus flux rates except during those periods when the rates were significantly different. The data were integrated for the 2-yr period to express changes at monthly intervals. The 196-day interval from 24 September 1974 to 7 April 1975 was carefully evaluated and adjusted to values of zero or near zero for this period

when no living material was apparent.

58. As a third means of estimating production via this method, Delaware and Georgia values were also adjusted when negative values of mortality or production were obtained. The procedure was based on the following criteria applicable to Equation 2, production and mortality estimates:

a. Values of r_i and X_i were utilized as accurate values related to detritus flux.

b. If production or mortality values were negative, the values were computed as follows:

   1) If Δb was positive and Δa was positive, X_i was assumed to be zero; mortality was equivalent to Δa; and production was $\Delta a + \Delta b$.

   2) If Δb was positive and Δa was negative, X_i was equal to Δa ; mortality was zero; and production was equal to Δb .

   3) If Δb was negative and Δa was negative, X_i was equal to the absolute value of $\Delta b + \Delta a$; mortality was equal to $X_i + (-\Delta a)$; and production was mortality plus $(-\Delta b)$.

   4) If Δb was negative and Δa was positive, X_i was equal to zero; mortality was Δa ; and production was $\Delta a + (-\Delta b)$.

59. The procedure described in the preceding paragraph was not utilized in more than 4 of the 14 samples in Delaware and Georgia for each species. These procedures were adopted from Smalley (1958) redefining the terminology in terms of Wiegert and Evans (1964).

Final estimates

60. Environmental metabolism and resultant variability of detritus flux rates were such that it was difficult to detect clear seasonal patterns for monthly productivity estimates. Therefore, in order to obtain expandable estimates, final net aerial primary production estimates were a result of averaging the values for all three methods utilized. The tidal variability that demanded this

treatment of the data is discussed in detail in the following section.

Frequency of inundation

61. Using a Zeiss Model Ni2 self-leveling level and a Philadelphia Model C metric rod, elevations from nearby benchmarks, corrected to tidal data from the nearest National Ocean Survey Primary Tide Stations, were run to adjacent salt marshes. Fifty elevations were taken within each stand at each location. Elevation frequency plots were constructed for each of the plants in each of the three locations relative to mean sea level (msl) and the percent of the tidal range (between mlw and mhw) above mlw. These elevations served to verify or cause rejection of earlier assumptions relative to the potential frequency of inundation.

62. Pertinent tidal and climatological data were obtained from the National Oceanographic and Atmospheric Administration (NOAA) for areas closest to the collection sites (Appendices A and B).

Test Results

Tidal influence

63. In order to adequately evaluate the Wiegert and Evans (1964) methodology, it was necessary to consider the tidal parameter influencing the plant stands. Maximum tidal range (3.20 m) was found in Maine (Table 4), where most of the plants were growing at elevations below mhw (none of the Delaware or Georgia plants except *Spartina cynosuroides* had their lower elevation limit below mhw). The plant frequency of occurrence for 50 elevation measurements in each stand is shown in Figures 18 through 20. For comparative purposes, these frequency distributions also include *Spartina alterniflora* (Delaware and Georgia), *Juncus roemerianus* (Georgia), *Salicornia virginica* (Delaware and Georgia), *Carex* sp. (Maine), and *Scirpus americanus* (Georgia). This information suggests that the potential of tidal influence is greatest in the Maine stands. This becomes a significant consideration in evaluating the net aerial primary production estimates utilizing the Wiegert and Evans (1964) method as will be discussed. In addition, the tidal amplitude suggests increased

Table 4

Elevation Ranges[f] Above Mean Low Water for Each Angiosperm and Its Sample Location Based on Tidal Datum

Angiosperm	Location		
	Maine[a]	Delaware[b]	Georgia[c]
B. frutescens	- -[g]	- -	2.25-2.49
D. spicata	- -	1.35-1.38	2.54-2.74
I. frutescens	- -	1.30-1.59	2.71-2.84
J. gerardii (C)[d]	2.94-3.95	- -	- -
J. gerardii (H)[e]	3.53-3.89	1.30-1.59	- -
P. communis	- -	1.42-2.96	- -
S. alterniflora (C)[d]	2.32-3.01	- -	- -
S. alterniflora (H)[e]	2.43-2.80	- -	- -
S. cynosuroides	- -	- -	2.13-3.16
S. patens	2.86-3.12	1.34-1.48	2.92-3.04
S. virginicus	- -	- -	2.90-3.11

[f] In metres.

[a] mhw = 3.20 m; mlw = 0.00 m.

[b] mhw = 1.25 m; mlw = 0.00 m.

[c] mhw = 2.13 m; mlw = 0.00 m.

[d] Creekbank.

[e] Highmarsh.

[g] Indicates plant species not present.

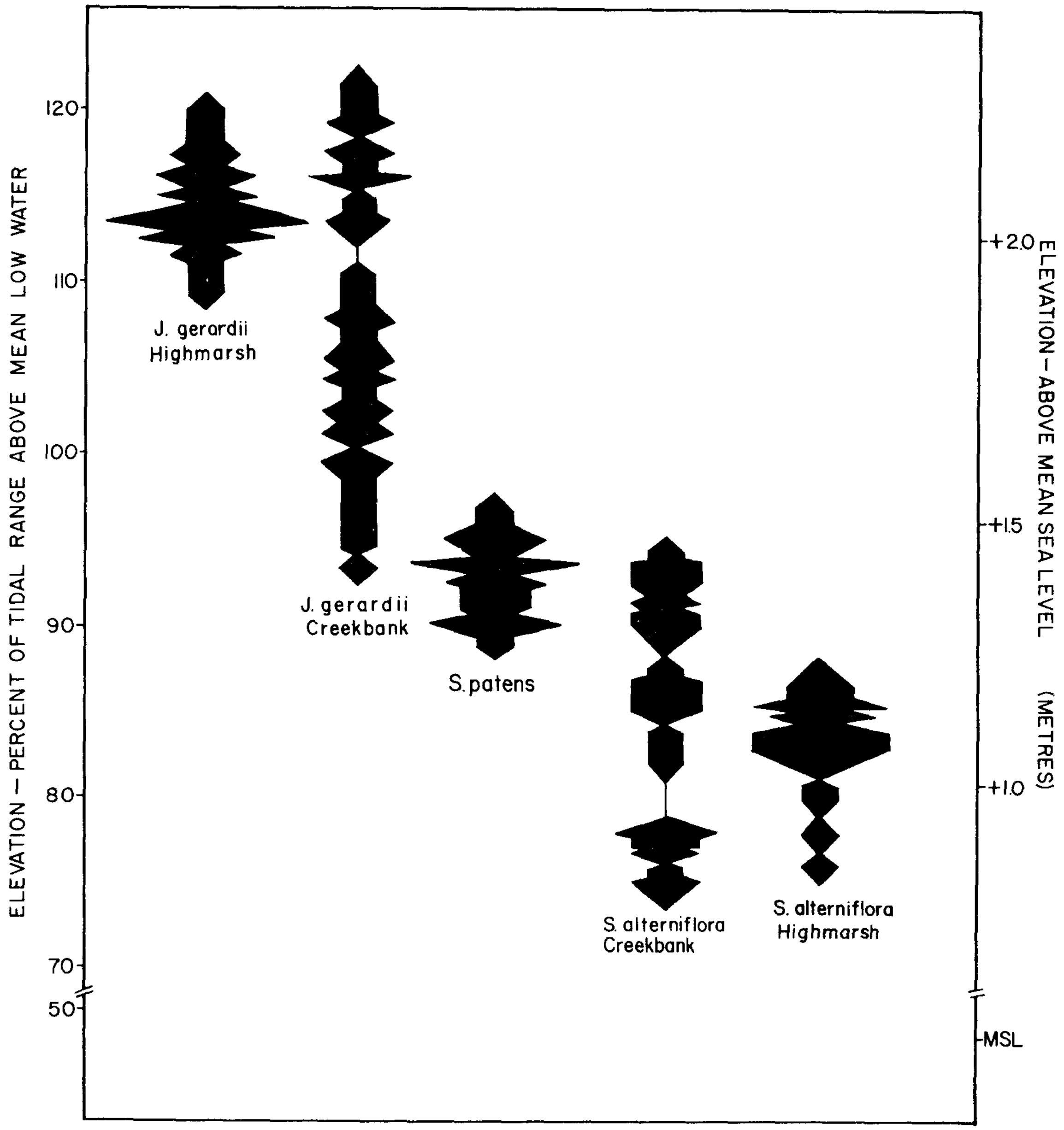
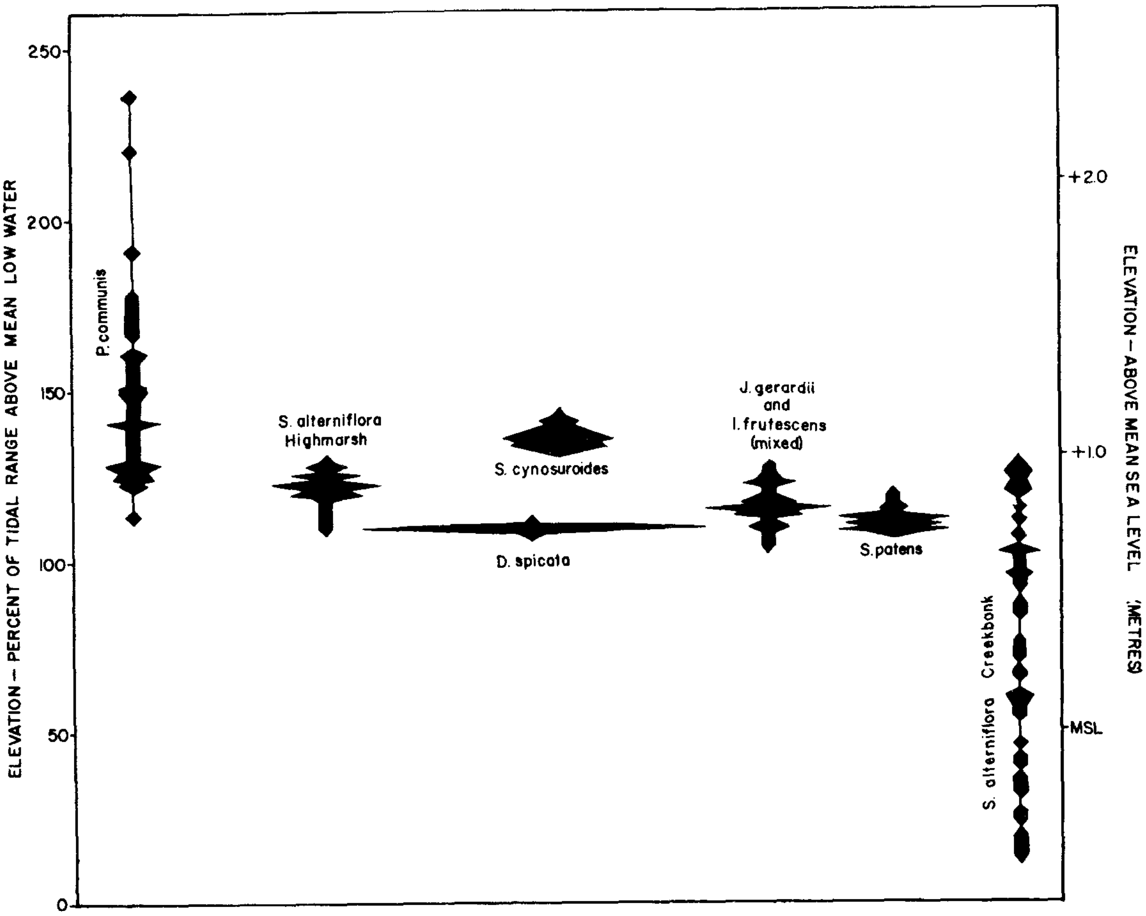


Figure 18. Salt marsh angiosperm plant elevation frequency distributions for Maine



PLANT ELEVATION FREQUENCY DISTRIBUTION FOR DELAWARE
SALT MARSH PLANTS

Figure 19. Salt marsh angiosperm plant elevation frequency distributions for Delaware

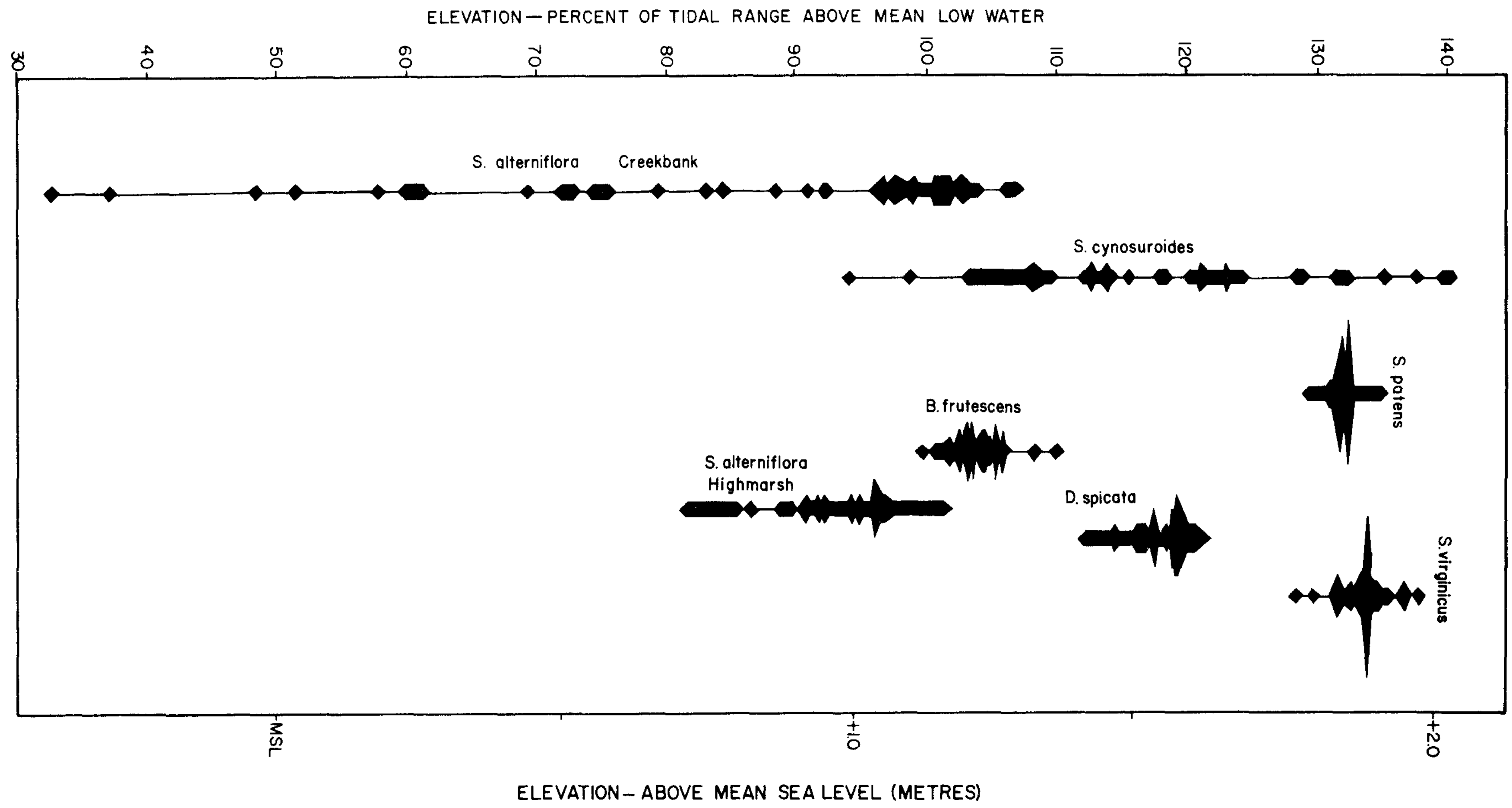


Figure 20. Georgia salt marsh plant elevation frequency distribution

potential of storm or spring tide flooding with increasing tidal amplitude.

Dead plot activity

64. A summary of w_0 and w_1 mean values (Table 5) was utilized to approximate the dead plot activity on an average basis. The method designed by Wiegert and Evans (1964) is effective only for those systems which are in a steady state. Information on w_0 and w_1 indicated that in all instances the initial dead sample (w_0) was greater than the second dead harvest (w_1) except in *Phragmites communis*. Thus, *Phragmites communis* was accumulating material at an estimated rate of 0.9 mg/g/day or 3.1 g/m^2/day. Its establishment on dredged material was apparently recent when compared to the other plant stands where *Distichlis spicata*, for example, only occurred in the oldest of marshes (Kerwin and Pedigo 1971). Therefore, it must be concluded that *Phragmites communis* is, at present, not in a steady state. One must assume that disappearance of the dead material would be mandatory to adjust for production during the year. Should such an occurrence not take place, instability of the stand is suggested.

Removal of dead material

65. The percent of w_0 which on an average basis for 2 yr disappeared (Table 5) in Maine generally indicated higher percentages that correspond directly with tidal amplitude and tidal elevations (Table 4) for these stands. The percentage of w_0 that disappeared in the Maine creekbank stands was twice that of the highmarsh stands. The steep slope and low elevation of the creekbank resulted in longer periods and increased frequency of inundation at these locations. Because of both the vertical rise and fall of the tides and horizontal flow over the stands, increased disappearance of dead material resulted.

66. The highest percent removal was in the creekbank *Spartina alterniflora*, which had the lowest elevation (Table 4) and greatest slope. The lowest percent removal in the five Maine stands was in the highmarsh *Juncus gerardii* where this angiosperm was noticeably separated from the other stands by a "*Juncus* levee" (Miller and

Table 5

Summary of Mean Dry Weight Data for the 2-yr Sample Period, Percent Removal of Dead Material in the Initial Sample, and Estimated Instantaneous Rates of Detritus Flux

Angiosperms and location	w_0(c) g/m^2	w_1(d) g/m^2	Average Percentage Removal	r_i(e) mg/g/day
MAINE				
Juncus gerardii (C)[a]	326	102	60	-
Juncus gerardii (H)[b]	90	58	34	-
Spartina alterniflora (C)[a]	78	12	84	-
Spartina alterniflora (H)[b]	373	218	42	-
Spartina patens	1281	751	41	-
DELAWARE				
Distichlis spicata	693	468	32	7
Juncus gerardii	400	245	39	9
Phragmites communis	3105	3276	-5	-1
Spartina patens	587	392	33	7
GEORGIA				
Distichlis spicata	742	389	48	12
Spartina cynosuroides	1357	988	27	6
Spartina patens	565	310	45	11
Sporobolus virginicus	109	40	63	18

[a] Creekbank.

[b] Highmarsh.

[c] w_0 = mean dead biomass of initial harvest

[d] w_1 = mean dead biomass at second harvest (56 days later)

[e] r_i = estimated instantaneous rate of detritus flux

Egler 1950) which allowed only the highest of tides to flood the site. The average percent removal was lowest in Delaware, again corresponding to the elevation of the stands and the tidal amplitude at this site.

67. It was also necessary to consider that assumably, the rate of decomposition is rapid for a longer period of time. This factor would suggest an increased percent removal in the Georgia site when compared to either Maine or Delaware. However, the removal percentages are more likely to be dominated by the effect of their respective tidal elevations in the Maine site, a parameter considered to be of greater significance than decomposition in Maine in dictating resultant disappearance of dead biomass. All of the sites were subject to extreme high tides that can significantly affect the rate at which dead material is removed for any given harvest interval.

Removal of live material

68. The influence of tidal movement required that the assumption of Wiegert and Evans (1964), regarding removal of the living material from the dead plot not significantly influencing the rate of disappearance, be questioned in these estuarine systems. Initially, most of these species were assumed to be highmarsh angiosperms where tidal influence would be minimal (Adams 1963), and such an assumption would be potentially valid. However, the elevation data clearly demonstrated (Figures 18-20) the invalidity of such an assumption, particularly in Maine. Therefore, the smallest possible sample size was utilized in instances where dense stands of stems were present (i.e., *Distichlis spicata*, *Juncus gerardii*, *Spartina patens*, *Spartina alterniflora*, and *Sporobolus virginicus*).

69. It was assumed that the removal of live material from a small plot within a dense stand would allow the remaining dead material to be carried only to the edge of the plot where it would meet substantial resistance. However, in Maine the tides submerged these plants more frequently (Table 5 and Figure 18) than the other sites (daily as opposed to sporadic occurrences), thus allowing the material to rise to the surface of the water and float free, thereby inflating the r_i values. These values are then relative values which coincide with

tidal amplitude activity and elevation limits of the angiosperms.

70. Tidal activity would tend to increase production estimates, particularly in Maine, since the removal of the living material at time t_0 altered the systém in a manner that decreased resistance to dead biomass removal by the tides. How much of an inflation this would cause needs further study; in addition, more frequent sampling is needed because of the short growth period and additional elevation data on each sample plot are needed. Elevation data by plot would allow a removal potential to be computed with respect to tidal influence and final values of production could be adjusted accordingly.

Detritus flux

71. The mean rates of detritus flux (Table 6) indicated that observations made concerning w_0 and w_1 values were valid (i.e., Maine generally had higher rates of flux followed by Georgia, then Delaware). The percent of the total r_i monthly means that were negative (Table 6) indicated similar results for all the stands. Only Delaware *Distichlis spicata* and Maine creekbank *Spartina alterniflora* had no negative r_i values. *Phragmites communis* had the most negative r_i values as might be expected based on its accumulation status.

72. Both heterogeneity of the areas and the potential for tides to move dead material into the dead plots could result in negative rates of detritus flux. Heterogeneity was probably a secondary cause when compared to tidal influence in this case. Mean rates of detritus flux (Table 6) were generally higher than the r_i values shown in Table 5. The r_i results in Table 5 were utilized only as an indication of the trends that might result in the r_i values. However, due to the variability of the r_i , it might best be computed by w_0 and w_1 means for the study period. The fact that r_i values were computed as an exponential loss rate may negate its validity as an appropriate component of the salt marsh system where erratic tidal influence would initiate a loss rate that could not be assured to be potential.

73. Most values of a (average dead biomass, Table 7) were in

Table 6

Summary of Instantaneous Rates of Detritus Flux Data and the Percentage of r_i Values That Were Negative by Species and Location

Angiosperms and locations	r_i mg/g/day Min.	Max.	Mean	Percentage Negative r_i values
MAINE				
Juncus gerardii (C)[a]	-10.0	65.9	32.4	14.3
Juncus gerardii (H)[b]	- 0.8	55.7	14.3	20.0
Spartina alterniflora (C)[a]	8.5	67.2	34.8	0.0
Spartina alterniflora (H)[b]	-10.3	30.9	12.3	33.3
Spartina patens	-13.3	84.0	14.5	33.3
DELAWARE				
Distichlis spicata	1.4	17.7	6.8	0.0
Juncus gerardii	- 9.6	27.1	8.6	21.4
Phragmites communis	-11.0	13.0	0.9	42.9
Spartina patens	- 0.8	52.8	11.3	7.1
GEORGIA				
Distichlis spicata	- 4.6	36.3	13.0	14.3
Spartina cynosuroides	-38.9	64.6	9.1	21.4
Spartina patens	- 1.3	30.3	11.6	14.3
Sporobolus virginicus	- 2.5	66.5	23.1	9.1

[a]Creekbank.

[b]Highmarsh.

Table 7

Summary of Dead Plant Biomass, Detritus Flux, Disappearance, Primary Production, and Mortality by Species and Location

Angiosperms	a	r_i	X_1	X_2	P_1	P_2	P_3	M_1	M_2
				MAINE*					
J. gerardii (C)**	483	32.4	3534	4096	3534	4097	5717	3534	4097
J. gerardii (H)+	113	14.3	485	744	485	777	592	485	777
S. alterniflora (C)**	135	34.8	1589	1589	1589	1589	1710	1589	1589
S. alterniflora (H)+	430	12.3	1789	1178	2200	1140	1829	1900	1279
S. patens	1368	14.5	5864	5738	5163	5738	7242	5564	5738
				DELAWARE					
D. spicata	721	6.8	1873	2127	1963	2234	1788	1898	2215
J. gerardii	462	8.6	1238	1831	1350	1867	1450	1278	1783
P. communis	2898	0.9	806	2688	272	3551	952	-229	4046
S. patens	678	11.3	2802	2928	2544	2676	2795	2664	2782
				GEORGIA					
D. spicata	798	13.0	4420	4600	4329	4526	3788	4322	4501
S. cynosuroides	1534	9.1	6132	5071	6898	5995	5095	6997	6045
S. patens	710	11.6	3650	3959	3978	4487	3007	3920	4377
S. virginicus	141	23.1	1424	1453	1424	1504	1188	1310	1394

NOTE: a = dead aerial plant material, g/m^2, computed from monthly means (Appendix C); r_i = instantaneous rates of detritus flux, mg/g/day, computed from monthly means inclusion of negative values (Appendix D); X = yearly estimation of dead biomass disappearance, $g/m^2/yr$, X_1 computed from monthly mean ($g/m^2/day$) times (365 days/yr) with negative values where present, and X_2 with modifications to eliminate negative values; P = net aerial production, $g/m^2/yr$, with P_1 computed with negative values where present, P_2 with modifications to eliminate negative values, and P_3 as a x r_i; and M = mortality by species and location, $g/m^2/yr$, with M_1 computed with negative values and M_2 with modifications to eliminate negative values.

*Maine X_1, X_2, P_1, P_2, M_1 and M_2 values were computed from integrated data with stipulations for X_1 and X_2 where appropriate.

**Creekbank.

+ Highmarsh.

excess of mean w_0 values (Table 5) since they included dead portions from living stems. Those values of w_0 which exceeded a values were a result of the averaging process. However, the close similarity between a and w_0 values indicated that the assumption made by Wiegert and Evans (1964) that the two plots (i.e., the clear-cut harvest plot and the adjacent dead plot) were identical was reasonable.

Disappearance of material

74. The importance of the instantaneous rates was observed when utilizing the rates to compute the amount of material disappearing (X_i) during the year. This procedure is heavily weighed by the average amount of dead material present during each interval and the instantaneous rate of detritus flux previously discussed. Values for X_1 (Table 7) portray the yearly estimates of material disappearing from each stand utilizing the observed r_i values for each interval. The high average rates do not always indicate high amounts of disappearance in Georgia, but the smallest amount of material disappearing. The value for *Sporobolus virginicus* was a result of material being removed by high tides, where the short height of the plant did not prevent material from rising and floating free.

75. Values for X_2 (Table 7) were computed utilizing the adjustment criteria discussed in the methods that deleted the influence of negative rates. In most instances, this procedure decreased the amount of dead material disappearing. Relative to the dead plots, this decrease was not accurately accounting for the material being removed. Because of increased potential removability (i.e., the absence of living material in the dead plots permitting increased tidal influence to remove excessive dead biomass), one additional sample in each of the three stands showing a decrease was altered to correct for this discrepancy. Maine *Spartina patens*, for example, indicated a disappearance of 1769.2 g/m^2 during the winter. This resulted in a winter production of 1556.2 g/m^2 when it was obvious that little or no production may occur in winter (Bernard, 1974). Therefore, production was assumed to be zero and the amount of material that disappeared during that interval was adjusted to 213.0 g/m^2. This value (213.0 g/m^2)

was computed by assuming the standing live biomass at time t_0 declined to zero ($a = -700\ g/m^2$), and this amount was contributed to the standing dead at time t_0 . Therefore, the disappearance was the adjusted change in dead biomass or 213.0 g/m^2. This situation provided additional evidence that the Wiegert and Evans (1964) methodology was overestimating Maine production, particularly when large time intervals separated the harvests. The *Spartina cynosuroides* alteration was employed to eliminate one extremely high value of disappearance that was in excess of the standing crop (live plus dead) and, therefore, unreasonable.

76. Since these alterations were necessary, in addition to alterations resulting from values with negative instantaneous rates of detritus flux and instances where negative production and mortality occurred, the percent of the total values used for X_1 that were altered to compute X_2 were calculated (Table 8). An examination of the X_1 and X_2 values (Table 7) and a consideration of the number of adjustments (Table 8) indicate the severity of those changes. The adjustments necessary which were not explained by the negative instantaneous rates of detritus flux are also indicated (Table 8). Most of the additional adjustments were computed because the change in dead standing crop was greater ($-\Delta a$) than the amount of dead material disappearing. In these instances, the instantaneous rate of detritus flux was an underestimate, which may create an overall balance of values over an extended period.

Primary productivity

77. Production values (P) were computed by three methods (Table 7). Values of P_1 were a result of adding both negative and positive values arithmetically based on monthly r_i values. Values of P_2 were estimated utilizing the Smalley (1958) modification as were the X_2 and M_2 values. Values of P_3 were a result of a computation suggested by Wiegert and Evans (1964) where an estimate of the mean dead biomass times the mean rate of disappearance was utilized. The highest variability in these values was in the *Phragmites communis* stand, which was determined earlier not to be in a steady

Table 8

Percent of Original Values Utilized for X_1 Which Needed Adjustments to Compute X_2 and Percent Not Explained by Negative Instantaneous Rates of Detritus Flux

	Maine		Delaware		Georgia	
Angiosperms	Adjusted Percent	Adjusted Excess Percent[c]	Adjusted Percent	Adjusted Excess Percent	Adjusted Percent	Adjusted Excess Percent
D. spicata	-	-	23.1	23.1	30.8	16.5
J. gerardii (C)[a]	28.6	14.3	-	-	-	-
J. gerardii (H)[b]	50.0	30.0	38.5	17.1	-	-
P. communis	-	-	72.7	29.8	-	-
S. alterniflora (C)[a]	0.0	0.0	-	-	-	-
S. alterniflora (H)[b]	50.0	16.7	-	-	-	-
S. cynosuroides	-	-	-	-	46.2	24.8
S. patens	57.0	33.3	23.1	16.0	30.8	16.5
S. virginicus	-	-	-	-	20.0	10.9

[a] Creekbank.

[b] Highmarsh.

[c] Adjusted excess unexplained by negative r_i

X_1 = yearly estimation of dead biomass computed from monthly means ($g/m^2/day$) times 365 (days/yr) with negative values present.

X_2 = yearly estimation of dead biomass computed from monthly means ($g/m^2/day$) times 365 (days/yr) with modifications to eliminate negative values.

state. Values for other species, although variable, were quite similar in comparison to those of *Phragmites communis*. Mortality values (Table 7) were computed as X_1 and P_1 as well as X_2 and P_2 for M_1 and M_2, respectively.

78. Those values observed in Table 9 are a result of averaging the values found in Table 7. Because of the differences between computation methods, averaging was necessary to adjust the estimates to one single estimate for each component in order to compute estimated production (EP) for Table 9. The EP value was computed on several assumptions:

- a. If the plant stand was in a steady state, then the amount of material being produced is equal to the amount of material being removed. This assumption was supported by the results of work done by Wiegert and Evans (1964) and Wiegert and McGinnis (1975).
- b. If the plant stand was in a steady state and in general the plants produced in a year die, then mortality should equal production. This assumption was supported by the data and by biomass information on the aerial portion of the plants investigated (Part II).

Therefore, these assumptions lead to the conclusion that X = M = P, i.e., the amount of material disappearing (X) is equal to the amount of material produced (P). Because of the variability involved in the procedures, it appeared most reasonable to average these final values to get an appropriate estimate of net aerial primary production.

79. The harvest procedure of Wiegert and Evans (1964) was initiated because it was believed that much of the influence of tidal inundation and decomposition was being overlooked by simply evaluating apparent production based on the living standing crop. To evaluate how much production potentially remains unnoticed by maximum standing crop methods, the maximum standing crop of living material (b , Table 9) was recorded. This value was divided into EP and the results were recorded in Table 9 (EP/b). Based on this procedure, much of the production computed here would have gone unnoticed. The validity of Georgia values was the most difficult to assess, since at no time during

Table 9

Mean Calculated Disappearance (X g/m^2/yr), Net Aerial Production (P g/m^2/yr), Mortality (M mg/m^2/yr), Estimated Production From Mean X, P, and M (EP g/m^2/yr), and Turnover Rate (EP/b per yr) By Species and Location

Angiosperms	X[a]	P[b]	M[c]	EP[d]	Max b[e]	EP/b
			MAINE			
J. gerardii (C)[f]	3815	4449	3816	4027	644	6
J. gerardii (H)[g]	614	618	614	616	244	3
S. alterniflora (C)[f]	1589	1629	1589	1602	431	4
S. alterniflora (H)[g]	1488	1756	1589	1611	245	7
S. patens	5801	6048	5651	5833	912	6
			DELAWARE			
D. spicata	2000	1995	2057	2017	1142	2
J. gerardii	1534	1556	1530	1540	560	3
P. communis	1747	1592	1909	1749	966	2
S. patens	2865	2672	2724	2754	962	3
			GEORGIA			
D. spicata	4510	4214	4412	4379	458	10
S. cynosuroides	5601	5996	6521	6040	2177	3
S. patens	3804	3824	4148	3926	980	4
S. virginicus	1438	1372	1352	1387	262	5

[a] Average dead material disappearance from Table 7.
[b] Average production from Table 7.
[c] Average mortality from Table 7.
[d] Estimated production from X, P, and M above.
[e] Maximum living biomass (dry wt g/m^2) from harvest data (Appendix C).
[f] Creekbank.
[g] Highmarsh.

the study did the living biomass decline to zero. Thus, it appeared that production continued throughout the year in Georgia during this study. Maine values clearly appeared to be overestimates of production; however, only a more complete evaluation of the r_i component would justify this assumption. Delaware turnover values were similar to those found by Kirby and Gosselink (1976) in their study of the Louisiana *Spartina alterniflora* marsh.

Discussion

80. The method outlined by Wiegert and Evans (1964), Reimold et al. (1975), Kirby and Gosselink (1976), and Gallagher et al. (In press) appears to approach the difficulties of estimating net primary production in a manner applicable to a grassland system. These procedures remain questionable in an estuarine system with environmental variables not present in the old field system for which the method was designed. It was felt that these data unquestionably show the influence of tidal activity and may negate the use of the exponential rate function r_i , which is a dominating component of the production estimates. Therefore, the assumptions that must be made for grasslands cannot be made in salt marshes; however, the estimates obtained from evaluating the dead material contributed to the estuarine system, either through tidal disappearance or decomposition, were necessary to examine the potential of an estuarine system (Kirby 1971).

81. Additional information must be gathered on the expected life span of individual plants considered in this study. With this additional information, one could feasibly examine the potential production of the estuarine plant species to compare to the estimates being gathered. Until such information is made available, it will be difficult to indicate the precision of these estimates. All of these values could be overestimates of net aerial primary production; however, since net aerial primary production values are all estimates, the true value remains to be validated for any location utilizing a method applicable to the marsh system.

82. Part IV compares estimated net primary production harvest

methodology indicating that no method presently developed is completely adequate for the estuarine ecosystem. Lomnicki et al. (1968) suggest a modification of the Wiegert and Evans method in which the dead material is removed in a manner that assumes that its removal does not significantly influence the rate of mortality. In the estuarine system this assumption might be more acceptable than those indicated by Wiegert and Evans (1964); however, to date, no one has verified the method for the salt marsh system.

83. Gallagher et al. (In press) suggested that the application of Wiegert and Evans (1964) methodology to marshes in the more northerly Atlantic coast sites would raise production estimates as it did in the lower latitudes. However, they also suggested that although production values would rise, the lower latitudes would still persistently have higher values. Latitude was suspected to have a significant influence on the performance of the plant species investigated; however, as suggested by Hatcher and Mann (1975), localized environmental parameters (e.g., nutrients and elevation) may be more directly responsible for growth when comparing a limited number of stands as in this study.

84. More information is required on the physiological responses of the plant species investigated here to determine optimum habitat. Such studies might conclude that the prevailing environmental metabolism of the Maine marshes may be more suitable for optimum growth of many of these plant species, thereby validating the results of this study.

85. Odum (1961) and Odum and Riedeburg (1976) suggested that "tidal subsidy" was important in categorizing production in height forms of *Spartina alterniflora*. Based on tidal elevation data of the plants investigated, this theory is supported by the resulting production estimates and it may apply to a much broader range of plants than suspected. However, discrepancies between values of apparently productive minor marsh plants and estimates of *Spartina alterniflora* production indicate that this theory may only hold for a single species in a localized area and not between species or widely varied locations. Although these primary productivity values are considerably higher than those previously published in the literature (Harper 1918, Waits 1967, Udell et al. 1969, Johnson 1970, Stuckey 1970,

Walton 1972, Gallagher and Reimold 1973, Nixon and Oviatt 1973a,b, Reimold et al. 1973, Wallentinus 1973), it appears that the present approach might more closely approximate the true net aerial primary production.

86. Kirby and Gosselink (1976) concluded that the Wiegert and Evans (1964) method possibly yielded the closest estimate to the true net aerial primary production, since other harvest methods commonly utilized in salt marsh systems are underestimates of net primary production. The Wiegert and Evans (1964) method was, however, observed to be a potential overestimate indicating that the true net aerial primary production, exclusive of leaching and herbivory, is an intermediate value between this method and others.

87. The complexity of the salt marsh system and the extreme variability between methodology (Kirby and Gosselink 1976, Part IV) provide evidence that more work is still required to acquire precise production estimates. Therefore, it appears that studies involving detailed and complex sampling that concentrate on the environmental parameters unique to the system are a necessity. Presently, the method designed by Wiegert and Evans (1964) used in conjunction with tidal data, physiological tolerance information on the plants being investigated, and knowledge of the system, in general, affords the most feasible means of obtaining more precise estimates. The estimates of this study must serve as a suggestion that net aerial primary production could be considerably higher than previously suggested in the literature.

LITERATURE CITED IN PART III

Adams, D. A. 1963. Factors influencing vascular plant zonation in North Carolina salt marshes. Ecology 44: 445-556.

Bernard, J. M. 1974. Seasonal changes in standing crop and primary production in a sedge wetland and an adjacent dry old field in Central Minnesota. Ecology 55: 350-359.

Blum, J. L. 1968. Salt marsh *Spartinas* and associated algae. Ecol. Monogr. 38: 199-221.

Bradbury, I. K. and G. Hofstra. 1976. Vegetation death and its importance in primary production measurements. Ecology 57: 209-211.

Chapman, V. J. 1940. Studies in salt marsh ecology, IV and VII. Comparisons with marshes on the east coast of North America. J. Ecol. 28: 118-152.

Chapman, V. J. 1974. Salt Marshes and Salt Deserts of the World. Leonard Hill Limited, London, Interscience Publishers, Inc., New York. 392 pp.

Clark, G. L. 1946. Dynamics of production in a marine area. Ecol. Monogr. 16: 322-335.

Conrad, H. S. 1935. The plant associations of central Long Island. Amer. Mid. Nat. 16: 433-516.

Daigh, F. C., D. MacGreary, and L. A. Stearns. 1938. Factors affecting the vegetation cover of Delaware marshes. Pp: 209-216. In: Proceedings of the Twenty-Fifth Annual Meeting of N. J. Mosquito Extermination Association.

Darnell, R. M. 1967. Organic detritus in relation to the estuarine ecosystem. pp. 376-382. In: Estuaries, G. H. Lauff (ed.). Publ. AAAS No. 83. Washington, D. C.

Davis, C. A. 1910. Salt marsh formation near Boston and its geological significance. Economic Geology 5: 623-639.

de la Cruz, A.A. 1965. A study of particulate organic detritus in a Georgia salt marsh estuarine ecosystem. Ph.D. Thesis. University of Georgia. 110 pp.

de la Cruz, A. A. 1973. The role of tidal marshes in the productivity of coastal waters. ASB Bulletin 29(4): 147-156.

Gallagher, J. L. and R. J. Reimold. 1973. Tidal marsh plant distribution and productivity patterns from the sea to fresh water - a challenge in resolution and discrimination. Pp. 165-184. In: Proceedings of the Fourth Biennial Workshop on Aerial Color Photography in Plant Sciences. University of Maine, Orono. July 10-12. Am. Soc. of Photogram.

Gallagher, J. L., R. J. Reimold, R. A. Linthurst, and W. J. Pfeiffer. In Press. Aerial production, mortality, and mineral accumulation dynamics in *Spartina alterniflora* and *Juncus roemerianus* in a Georgia salt marsh. (Ecology).

Ganong, W. F. 1903. The vegetation of the Bay of Fundy salt and diked marshes. Botan. Gaz. 36: 161-186, 280-302, 349-367, 429-455.

Good, R. E. 1965. Salt marsh vegetation, Cape May, New Jersey. Bull. New Jersey Acad. Sci. 10: 1-11.

Harper, R. M. 1918. Some dynamic studies of Long Island vegetation. Plant World 21: 38-46.

Harshberger, J. W. 1911. An hydrometric investigation of the influences of sea water on the distribution of salt marsh and estuarine plants. Proc. Amer. Phil. Soc. 50: 457-496.

Hatcher, B. G. and K. H. Mann. 1975. Aboveground production of marsh cordgrass (*Spartina alterniflora*) near the northern end of its range. J. Fish. Res. Bd. Can. 32: 83-87.

Heald, E. J. 1969. The production of organic detritus in a south Florida estuary. Ph.D. Thesis, University of Miami, Miami, Fla. 110 pp.

Jackson, C. R. 1952. Some topographic and edaphic factors affecting plant distribution in a tidal marsh. Quart. Journ. Fla. Acad. Sci. 57: 795-804.

Jannasch, H. W. and G. E. Jones. 1959. Bacterial populations in sea water as determined by different methods of enumeration. Limnol. Oceanogr. 4: 128-139.

Johnson, D. S. and H. H. York. 1915. The relation of plants to tide levels. Carnegie Inst. Wash. Publ. 206. 162 pp.

Johnson, M. 1970. Preliminary report on species composition, chemical composition, biomass, and production of marsh vegetation in the upper Patuxent Estuary, Maryland. Chesapeake Biological Laboratory. Ref. No. 70-130, pp. 165-178.

Keefe, C. W. 1972. Marsh production: A summary of the literature. Contr. in Mar. Sci. 16: 164-181.

Kerwin, J. A. and R. A. Pedigo. 1971. Synecology of a Virginia salt marsh. Chesapeake Sci. 12: 125-130.

Kirby, C. J., Jr. 1971. The annual net primary production and decomposition of salt marsh grass *Spartina alterniflora* Loisel. in the Barataria Bay estuary of Louisiana. Ph.D. Thesis. Louisiana State University. 74 p.

Kirby, C. J. and J. G. Gosselink. 1976. Primary production in a Louisiana gulf coast *Spartina alterniflora* marsh. Ecology 57: 1052-1059.

Kurz, H. and K. Wagner. 1957. Tidal marshes of the Gulf and Atlantic coasts of northern Florida and Charleston, South Carolina. Florida State Univ. Stud. 24, 168 p.

Lomnicki, A., E. Bandala, and K. Jankowska. 1968. Modification of the Wiegert-Evans method for estimation of net primary production. Ecology 49: 147-149.

Mendelssohn, I. A. and K. L. Marcellus. 1976. Angiosperm production of three Virginia marshes in various salinity and soil nutrient regimes. Chesapeake Sci. 17: 15-23.

Miller, W. R. and F. E. Egler. 1950. Vegetation of the Wequetequock-Pawcatuck tidal marshes, Connecticut. Ecol. Monogr. 20: 143-172.

Morgan, M. H. 1961. Angiosperm production on a salt marsh. M. S. Thesis, University of Delaware, Newark. 34 p.

Nixon, S. W. and C. A. Oviatt. 1973a. Analysis of local variation in the standing crop of *Spartina alterniflora* . Bot. Mar. 16: 103-109.

Nixon, S. W. and C. A. Oviatt. 1973b. Ecology of a New England salt marsh. Ecol. Monogr. 43: 463-498.

Odum, E. P. 1961. The role of tidal marshes in estuarine production. The N. Y. State Conservationist 15: 12-15.

Odum, E. P. and A. A. de la Cruz. 1963. Detritus as a major component of ecosystems. AIBS Bull. 13: 39-40.

Odum, E. P. and A. A. de la Cruz. 1967. Particulate organic detritus in a Georgia salt marsh estuarine ecosystem. Pp. 383-388. In: Estuaries. G. H. Lauff (ed.). Publ. AAAS No. 83. Washington, D. C.

Odum, E. P. and C. H. Riedeburg. 1976. A dye study of interstitial water flow in tidal marsh sediments. In: Abstracts of papers submitted for the 39th Annual Meeting ASLO, Skidaway Institute of Oceanography, Savannah, Ga.

Penfound, W. T. and E. S. Hathaway. 1938. Plant communities in the marshlands of southeastern Louisiana. Ecol. Monogr. 8: 1-56.

Redfield, A. C. 1965. Onotogeny of a salt marsh estuary. Science 147: 50-55.

Redfield, A. C. 1972. Development of a New England salt marsh. Ecol. Monogr. 42: 201-237.

Reimold, R. J. 1976. Mangals and salt marshes of eastern United States. Pp. 393-406. In: V. J. Chapman (ed.) Wet Coastal Ecosystems. Elsiver Scientific Publ. Co., Amsterdam.

Reimold, R. J., J. L. Gallagher, and D. E. Thompson. 1973. Remote sensing of tidal marsh. Photogram. Eng. Vol. 39(5): 477-488.

Reimold, R. J., J. L. Gallagher, R. A. Linthurst, and W. J. Pfeiffer. 1975. Detritus production in coastal Georgia salt marshes. In: Estuarine Research. Vol. II. E. Cronin (ed.). Academic Press, Inc., New York. pp. 217-228.

Riley, G. A. 1963. Organic aggregates in sea water and the dynamics of their formation and utilization. Limnol. Oceanogr. 8: 372-381.

Schelske, C. L. and E. P. Odum. 1961. Mechanisms for maintaining high productivity in Georgia estuaries. Bull. Gulf and Carib. Fish Inst. 14: 75-80.

Singh, J. S., W. K. Lavenroth, and R. K. Steinhorst. 1975. Review and assessment of various techniques for estimating net aerial primary production in grasslands from harvest data. Bot. Rev. 41: 181-232.

Smalley, A. E. 1958. The role of two invertebrate populations, *Littorina irrorata* and *Orchelimum fidicinum* in the energy flow of a salt marsh ecosystem. Ph. D. Thesis. University of Georgia. Athens. 126 pp.

Snedecor, G. W. and W. G. Cochran. 1967. Statistical Methods. The Iowa State University Press, Ames, Iowa. 593 pp.

Stroud, L. M. and A. W. Cooper. 1968. Color-infrared aerial photographic interpretation and net primary productivity of a regularly flooded North Carolina salt marsh. Water Resources Research Inst. Report No. 14, North Carolina State University at Raleigh. 86 pp.

Stuckey, I. H. 1970. Measuring the productivity of salt marshes. Maritimes 14(1): 9-11.

Taylor, N. 1938. A preliminary report on the salt marsh vegetation of Long Island, New York. Bull. N. Y. Stat. Mus. 316: 21-84.

Teal, J. M. 1962. Energy flow in the salt marsh ecosystem of Georgia. Ecology 43: 614-624.

Udell, H. F., J. Zarudsky, T. E. Doheny, and P. R. Burkholder. 1969. Productivity and nutrient values of plants growing in the salt marshes of the town of Hempstead, Long Island. Bull. Tor. Bot. Club 96: 42-51.

Waits, E. D. 1967. Net primary productivity of an irregularly flooded North Carolina salt marsh. Ph.D. Thesis, North Carolina State University at Raleigh. 113 pp.

Wallentinus, H. G. 1973. Aboveground primary production of *Juncus gerardii* on a Baltic seashore meadow. Oikos 24: 200-219.

Walton, T. E. 1972. Primary productivity, succession, and management of a New Jersey coastal marsh. Master's Thesis, Graduate School of Fine Arts, University of Pennsylvania, Philadelphia. 128 p.

Wentz, W. A., R. L. Smith, and J. A. Kadlec. 1974. A selected annotated bibliography on aquatic and marsh plants and their management. School of Natural Resources, University of Michigan, Ann Arbor. 190 pp.

Wiegert, R. G. 1962. The selection of an optimum quadrat size for sampling the standing crop of grasses and forbs. Ecology 43: 125-129.

Wiegert, R. G. and F. C. Evans. 1964. Primary production and the disappearance of dead vegetation on an old field in southeastern Michigan. Ecology 45: 49-63.

Wiegert, R. G. and J. T. McGinnis. 1975. Annual production and disappearance of detritus on three South Carolina old fields. Ecology 56: 129-140.

Wiegert, R. G., R. R. Christian, J. L. Gallagher, J. R. Hall, R. D. H. Jones, and R. L. Wetzel. 1975. A preliminary ecosystem model of coastal Georgia *Spartina* marsh. pp 583-601. In: L. E. Cronin (ed.), Estuarine Research. Academic Press, Inc., New York.

PART IV: EVALUATION OF NET AERIAL PRIMARY PRODUCTION ESTIMATION METHODOLOGY FOR SELECTED ESTUARINE MACROPHYTES

Introduction

88. Common to most ecological studies is an analysis of the metabolic activity of the primary producers in terms of net primary production. Resulting values of annual net primary production (ANPP) are questionably comparable because of temporal, spatial, and methodology differences. As ecosystem modeling becomes more refined, comparisons of various systems will be useful. Therefore, it is necessary that considerable emphasis be placed on methodology related to the collection and treatment of data so that systems analysis comparisons are feasible.

89. The problem of employing different techniques to estimate a single component of a system appears to be more and more obvious in the literature. The problem is confined not only to different techniques for different systems, but it is common to see various methodologies to evaluate a similar system in two locations. The salt marsh-estuarine system is no exception.

90. Kennedy (1972), Singh and Yadava (1974), and Singh et al. (1975) have assessed methods of estimating ANPP in grasslands. Their approach has been statistical as well as biological in order to determine the best and most comparable methods presently available.

91. The relationship for each method used by Singh et al. (1975) in the grasslands is not necessarily applicable to the estuarine system where additional environmental parameters (e.g. the tides) are a significant influence. Kirby (1971) has discussed advantages and disadvantages of a variety of methods utilized in wetland systems. However, to date, no standard method is utilized in either system, grasslands or wetlands.

92. This part of the report evaluates several methods of ANPP estimation and presents the resulting quantitative data for a number of salt marsh macrophytes in Maine, Delaware, and Georgia. A statistical approach has not been taken; however, the resulting data will allow comparisons of presently existing values of estimated

net aerial primary production for salt marsh angiosperms. In addition, the extreme ranges produced by the methodology will be an attempt to support the need for a standard method with considerations of acquiring the most accurate and ecologically meaningful estimates.

Methods

93. Information necessary to compute production for six salt marshes along the eastern coast of the United States (Maine, Delaware, and Georgia) was collected. Selection criteria and site locations for obtaining that information in the field were reported in Parts II and III. Aerial plant material was harvested utilizing contiguous paired plots as described by Wiegert and Evans (1964) and Reimold et al. (1975) (see Part II and Part III). The angiosperms chosen for investigation and their location are shown in Table 10. Seasonal biomass information and seasonal production results based on Wiegert and Evans (1964) methodology were presented in Part III. Only monospecific stands of plant species were evaluated in these studies.

94. Five methods of computing annual net production in salt marsh systems were selected for comparison. The difficulties of placing appropriate statistical tests on production estimates are well known. Therefore, it was assumed that the values to be presented were relative values, representative of the angiosperms investigated. The information collected for each angiosperm was dependent on identical technique and measurement of identical components for each species. For the purpose of the discussion, it was assumed that the monthly averages were without error, an assumption that will be discussed later.

95. All data collected from Maine were integrated to produce data at monthly intervals for 1 yr (Part III). *Phragmites communis*, *Sporobolus virginicus*, and *Iva frutescens* (Georgia) data were utilized from February 1974 through January 1975 because of late initiation of samples in the *Sporobolus virginicus* and *Iva frutescens* stands and because of site relocation of *Phragmites communis*. All other data were bimonthly samples collected from 27 August 1973 through 25 August 1975 and the resulting ANPP values were divided by two to get an

Table 10

Angiosperms Evaluated and Their Geographic Location

Angiosperms	Location[a]		
Borrichia frutescens			G
Distichlis spicata		D	G
Iva frutescens		D	G
Juncus gerardii (C)[b]	M		
Juncus gerardii (H)[c]	M	D	
Phragmites communis		D	
Spartina alterniflora (C)[b]	M		
Spartina alterniflora (H)[c]	M		
Spartina cynosuroides			G
Spartina patens	M	D	G
Sporobolus virginicus			G

[a]M = Maine, D = Delaware, G = Georgia

[b]Creekbank.

[c]Highmarsh.

average ANPP for the 2-yr period.

Review of ANPP Methodology

96. An excellent review of ANPP methodology was presented by Singh et al. (1975) with relation to grassland systems. The methodology presented there does not change for the estuarine system; however, interpretation and criticism of the results varied. Therefore, only those methods utilized in this study are briefly presented in terms of basic methodology for convenience of comparison. In addition, a more recent ANPP estimate procedure developed by Valiela et al. (1975) is also discussed here.

Method 1 - peak standing crop

97. Method 1 entailed selecting the peak standing crop of living material from the harvest data for each year, taking the mean of the two peaks, and utilizing the resulting value as the ANPP value. Since plants of the nature studied gain and lose leaves throughout the season, this method was considered to result in an underestimate of ANPP. This procedure is commonly used in agriculture to determine yields of economically important crops (Milner and Hughes, 1968).

Method 2 - Milner and Hughes (1968)

98. Method 2, suggested by Milner and Hughes (1968), involved summing the positive changes in the standing crop of living material (Δb) between intervals for a 1-yr period. The equation is presented by:

$$\mathrm{ANPP} = \sum_{i=1}^{n} (\Delta b_i) \tag{3}$$

Method 3 - Smalley (1958)

99. Method 3, presented by Smalley (1958), is the most widely used method of net production estimation utilized in marsh systems (Kirby 1971). Determinations of both living and dead standing crop biomass were utilized and production was computed as follows:

<u>a</u>. If there were both an increase in the standing crop of living material and an increase in standing crop of dead biomass, the net production was the sum of the

increases.

b. If both living and dead standing crops decreased, then production was zero.

c. If the standing crop of living biomass increased and the standing crop of dead biomass decreased, production was equal to the increase in the living material.

d. If the amount of dead material increased and the amount of living biomass decreased, they were added algebraically; if the result was negative, production was zero; and if the result was positive, the resulting value was equal to production.

The sum of the resultant values for the above assessment represents ANPP.

Method 4 - Valiela et al. (1975)

100. Method 4, presented by Valiela et al. (1975), was a procedure involving cumulative measurements of production in a sequence of sampling intervals. They determined that the standing crop varied little from year to year; therefore, the sum of the losses of dead material over a growing season should equal net annual aboveground production. This was a necessary assumption because growth, death, and disappearance of dead material took place between their sampling intervals. The amount of plant biomass e that died and was not included as dead standing crop was calculated as follows:

$$e = -\Delta d, \text{ if } \Delta l > 0 \text{ and } \Delta d < 0 \qquad (4)$$

$$e = (\Delta l + \Delta d), \text{ if } \Delta l < 0 \qquad (5)$$

where Δl was the change in live standing crop between any two sampling dates and Δd was the change in standing dead material for the same interval.

101. Values of e could never be negative because Valiela et al. assumed that only live biomass in the plots contributed to the standing dead material component. Therefore, should a negative e result, the values were set equal to zero. The e values computed were summed to get estimated yearly production.

Method 5 - Wiegert and Evans (1964)

102. Method 5, suggested by Wiegert and Evans (1964), was the most involved procedure utilized. This procedure was specifically designed for grassland systems; however, it had recently been utilized in wetlands (Reimold et al. 1975, Gallagher et al. In press). This method requires an additional consideration, relative to the other methods, in computing ANPP (i.e., the disappearance of dead material).

103. Wiegert and Evans suggested that if the dead material is removed from a given area and weighed w_0 at time t_0, and if the dead material from a second area identical in size to the first is removed and weighed w_1 at time t_1, the instantaneous rate of disappearance of dead material from these plots could be computed as:

$$r_i = \ln \frac{(w_0/w_1)}{t_1 - t_0} \qquad (6)$$

where r_i = disappearance rate, g/g/day, and $(t_1 - t_0)$ is in days.

104. To minimize the error involved in the paired-plots method, the living vegetation on each of the two paired quadrats was removed by selective clipping. Quadrats were paired in a manner such that they shared a common border. One plot was then selected at random and the dead material was removed w_o. After a known time interval $t_1 - t_0$, the site was revisited and the dead material was removed from the remaining plot w_1.

105. Utilizing these results, the amount of dead material disappearing during an interval X_i was computed as follows:

$$X_i = [(a_i + a_{i-1})/2]\ r_i t_i \qquad (7)$$

where a_i = standing dead material at the end,

a_{i-1} = standing dead material at start,

t_i = interval, days.

106. Changes in standing crops of living (Δb_i) and dead material (Δa_i), respectively, were computed as follows:

$$\Delta b_i = b_i - b_{i-1} \qquad (8)$$

$$\Delta a_i = a_i - a_{i-1} \qquad (9)$$

107. Finally, mortality d_i was computed as:

$$d_i = X_i + a_i \tag{10}$$

and production Y_i was computed as:

$$Y_i = b_i + d_i \tag{11}$$

The sum of the Y_i values results in an estimate of ANPP.

Results and Discussion

108. A summary of maximum and minimum live and dead standing crops for the plants evaluated is presented in Table 11. The resulting estimates of ANPP by method (Table 12) should be utilized to clarify the following discussion.

Method 1

109. Method 1 (Peak Standing Crop) assumes that there is no carry-over of living material from one year to the next. The assumption would be valid for Delaware and Maine, but not for Georgia. Therefore, not only geographical location must be considered, but a consideration of the morphology of plant species is also necessary. *Borrichia frutescens* and *Iva frutescens* were woody plants and carry-over of living material occurred. Therefore, as suggested by Ovington et al. (1963) and Singh and Yadava (1972), the lowest value of standing crop should be subtracted to account for carry-over growth. Since the method did not take into account mortality between harvest intervals nor did it consider disappearing material between intervals, it results in a severe underestimate of net aerial primary production.

Method 2

110. Method 2 (Milner and Hughes 1968) resulted in ANPP estimates that were lower in Georgia than those for Method 1. This was a direct result of the living component never declining to a zero biomass value. Therefore, the increment differences were small in relation to the maximum living material present at any single peak. In Delaware and Maine, the ANPP estimates from Methods 1 and 2 were nearly identical. This was again in response to the living component which declined to zero during the winter. Therefore, the sum of the

Table 11

Summary of Minimum, Maximum, and Ranges for Dry Weights of Living and Dead Aerial Plant Material by Species and Location

Angiosperms	Live Material Min	Live Material Max	Live Material Range	Dead Material Min	Dead Material Max	Dead Material Range
Maine						
J. gerardii (C)[a]	0	644	644	34	1050	1016
J. gerardii (H)[b]	0	244	244	22	432	410
S. alterniflora (C)[a]	0	431	431	20	431	411
S. alterniflora (H)[b]	0	245	245	187	641	454
S. patens	0	912	912	132	2124	1992
Delaware						
D. spicata	0	1142	1142	248	1302	1054
I. frutescens	427	1491	1064	107	565	458
J. gerardii	0	560	560	182	748	566
P. communis	0	965	965	1464	3051	1587
S. patens	0	962	962	354	962	608
Georgia						
B. frutescens	648	1860	1212	184	291	107
D. spicata	128	458	330	331	1260	929
I. frutescens	116	1288	1172	538	1396	858
S. cynosuroides	4	2176	2172	291	2584	2293
S. patens	176	980	804	236	1324	1088
S. virginicus	39	262	223	80	316	236

[a]Creekbank.

[b]Highmarsh.

NOTE: All measurements are in g/m^2.

Table 12

Values of ANPP by Method, Location, and Species

Angiosperms	Method by location[c]				
	1	2	3	4	5
Maine					
J. gerardii (C)[a]	644	634	1940	1940	4027
J. gerardii (H)[b]	244	244	562	463	616
S. alterniflora (C)[a]	431	431	758	758	1602
S. alterniflora (H)[b]	246	246	763	662	1611
S. patens	912	912	3523	3523	5833
Delaware					
D. spicata	856	864	1274	1191	2017
I. frutescens	1372	1319	1723	1633	-
J. gerardii	524	524	884	775	1540
P. communis	920	965	1501	3203	1749
S. patens	807	522	980	1241	2753
Georgia					
B. frutescens	1555	1045	1119	1379	-
D. spicata	395	283	1258	988	4378
I. frutescens	1227	1023	1847	2298	-
S. cynosuroides	1920	1866	2789	1742	6039
S. patens	946	705	1674	1028	3925
S. virginicus	262	220	316	447	1387

[a]Creekbank.

[b]Highmarsh.

[c]Numbers refer to method numbers as cited in text.
NOTE: All values presented in grams per square metre per year.

positive increments of changing living biomass (Method 2) was equal to the peak standing crop (Method 1). *Spartina patens* in Delaware presents a potential discrepancy in this theory. Although the standing live component did decline to zero during the winter, the peak standing crop value for Delaware *Spartina patens* (Method 1) was unusually high because the initial two samples from year one yielded large biomass values. If the biomass of living material was ignored for the initial samples, then the peak average would be 487.3 g/m^2, a value comparable to Method 2. These large peak values occurred at the end of the growing season in the Delaware *Spartina patens;* therefore, no positive increments of change in living material were contributed to Method 2 procedures at this time.

Method 1 vs. Method 2

111. The consistency between Methods 1 and 2 is shown in the Maine samples (Table 12). *Juncus gerardii* (C) ANPP was lower in Method 2 because no sample collected resulted in a zero biomass component. However, if one assumed that this component did go to zero, then 10 g of material would be added to Method 2. Milner and Hughes (1968) suggested that their method was an underestimate of production because death of living material between harvests was not considered. In addition, it appears this method must be cautiously used only in areas where an annual turnover is visually apparent.

Method 3

112. Method 3 (Smalley 1958) was consistently higher in all instances than either Method 1 or 2. This method (3) was more acceptable in theory than the other methods considered thus far because it attempted to account for the mortality of living material, a necessary consideration. However, it did not account for the new shoot growth during periods of rapid decline in mature live standing crop when no apparent increase in the dead component resulted because of decomposition and tidal removal of that material. Although the importance of tidal flushing losses and decomposition is recognized by most researchers, Smalley's method has been historically prominent in the literature. The resulting ANPP values indicate that this method (3)

produced the results expected based on tidal elevations of the plant species, their exposure, and the appearance of the stands (Parts II and III).

Method 4

113. Method 4 (Valiela et al. 1975) attempts to compensate for death and disappearance of dead material during the harvest intervals. The method was designed for an area where the litter component of dead material was negligible. None of the areas sampled for this study had a negligible litter base except the woody plants, *Borrichia frutescens* and *Iva frutescens*. In addition, the method did not evaluate growth directly unless there were increases in dead matter. If the living biomass increased while some living plants died concomitantly, and no change in the standing dead was apparent, a potential occurrence because of tidal flushing, then this growth remained unassessed. Further, it must be considered that the method assumes that the system being evaluated is a steady state such that the amount of material produced is equal to the amount of material that disappeared. Finally, Method 4 does not permit seasonal growth patterns to be distinguished, since unmeasured growth (increase in living biomass) during a harvest interval is not detected until decreases in dead material were apparent at a later interval. Valiela et al. (1975) suggested that their method was an underestimate based on the above difficulties and fully recognized its limitations.

Method 3 vs. Method 4

114. Over 30 percent of all resulting ANPP values yielded greater values for Method 4 than Method 3. Both methods had inherent difficulties; however, the benefit of seasonal results was a positive aspect of Method 3. In addition, the potential of inaccurately measuring the dead component when litter was prevalent (Method 4) appeared greater than the potential of inaccurately measuring standing living material (Method 3). Therefore, Method 3, which measured the living biomass directly, was considered to be more reliable than Method 4. *Spartina cynosuroides* ANPP determined by Method 4 was less than the peak standing crop of living material. Enough biomass information is

available (Table 11) to imply that Method 4 severely underestimated the production of this plant. With plants growing above mhw (Part III) dead material has the potential to accumulate for some time before tidal flushing takes place. Method 4 had a greater potential to be affected by this occurrence than did Method 3, which would account for the occurrence more directly. Both estimates (i.e., Methods 3 and 4) were considered to be underestimates, both were plagued with inherent difficulties, and both resulted in similar estimates.

Method 5

115. Method 5 (Wiegert and Evans 1964) was more difficult to evaluate for specific shortcomings. However, it was potentially the most questionable method to use for the marsh system since it was the only method that potentially overestimated net production exclusive of herbivore grazing and leaching of material (Part III). Several assumptions were necessary to compute the instantaneous rate of detritus flux, and these assumptions were found to be extremely influential in the resulting ANPP values. The assumptions and explanations are as follows:

- a. Both paired plots were identical. Since these data were from monospecific stands, this assumption appeared reasonable (Part III).
- b. The removal of dead material did not influence the rate of disappearance. This assumption could not be made in the marsh system under tidal influence. In dense stands of living plants, the removal of the living material resulted in an increased potential for tidal removal of the remaining dead during the harvest interval. Coincidentally, this method may have also decreased the potential for rapid decomposition (Wiegert and Evans 1964), providing somewhat of a counter response to the tidal removal.
- c. No additional material could be contributed to the dead material of the plot where the living material

was selectively removed at t_0. This assumption could not be made in the estuarine system, again because of tidal influence that had the capability to transfer dead material from one plot to another. Negative rates of disappearance appeared to be a direct result of the invalidity of this assumption. This also indicates that growth and mortality cannot occur during the harvest period.

d. The method assumes that the ecosystem being investigated is stable, and that utilizing values of milligrams are accurate in harvest data (Singh et al. 1975).

A more complete evaluation of this method was presented in Part III.

Comparison of methods

116. The values of ANPP used in Table 11 were presented in Part II after modifications of Wiegert and Evans (1964) methodology indicated in that section. The values presented were considered to be the best estimates of these species' ANPP's, utilizing the logic presented by Wiegert and Evans (1964). In all instances except for *Phragmites communis*, Method 5 produced higher values for ANPP than any other method. Results utilizing Method 5 suggested that the *Phragmites communis* stand was unstable (Part III) where material was apparently accumulating. Method 4 produced a higher value of ANPP for *Phragmites communis* where it, in opposition to Method 5 results, indicated that material was rapidly disappearing. If the area was not a stable ecosystem, then neither method was applicable, based on assumptions that must be made in both Methods 4 and 5.

117. Selected method ratios (Table 13) are presented for rapid comparison of methods on a relative basis. The mean ratio and standard error ($\bar{x} \pm s_{\bar{x}}$) for each comparison is also presented (Table 13), which indicates similarities of comparisons among locations for method ratios 1:2, 2:3, and 3:4 relative to those values for method ratio 4:5. The comparisons of Methods 4 and 5 showed more pronounced differences between locations based on mean values.

118. A more appropriate comparison might be that of the most

Table 13

Method Ratios by Location and Species

Angiosperms	Ratios* 1:2	2:3	3:4	4:5
Maine				
J. gerardii (C)[a]	1.0	0.3	1.0	0.5
J. gerardii (H)[b]	1.0	0.4	1.2	0.8
S. alterniflora (C)[a]	1.0	0.6	1.0	0.5
S. alterniflora (H)[b]	1.0	0.3	1.2	0.4
S. patens	1.0	0.3	1.0	0.6
$\bar{x} \pm s_{\bar{x}}$	1.0 ± 0.0	0.4 ± 0.2	1.1 ± 0.0	0.6 ± 0.1
Delaware				
D. spicata	1.0	0.7	1.1	0.6
I. frutescens	1.0	0.8	1.0	-
J. gerardii	1.0	0.6	1.1	0.5
P. communis	1.0	0.6	0.5	1.8
S. patens	1.5	0.5	0.8	0.5
$\bar{x} \pm s_{\bar{x}}$	1.1 ± 0.1	0.6 ± 0.1	0.9 ± 0.1	0.9 ± 0.3
Georgia				
B. frutescens	1.5	0.9	0.8	-
D. spicata	1.4	0.2	1.3	0.2
I. frutescens	1.2	0.5	0.8	-
S. cynosuroides	1.0	0.7	1.6	0.3
S. patens	1.3	0.4	1.6	0.3
S. virginicus	1.2	0.7	0.7	0.3
$\bar{x} \pm s_{\bar{x}}$	1.3 ± 0.1	0.6 ± 0.1	1.1 ± 0.2	0.3 ± 0.1

*1:2 = peak standing crop vs. Milner and Hughes (1968) Methodology; 2:3 = Milner and Hughes (1968) Methodology vs. Smalley (1958) Methodology; 3:4 = Smalley (1958) vs. Valiela et al. (1975) Methodology; and 4:5 = Valiela et al. (1975) vs. Wiegert and Evans (1964) Methodology.

[a]Creekbank.

[b]Highmarsh.

widely used method, Smalley (1958), and those values computed based on the methodology of Wiegert and Evans (1964). Excluding the *Phragmites communis* values, Method 5 (Wiegert and Evans 1964), on an average basis, resulted in ANPP estimates 3.1 ($\pm$ 1.1) times greater than Method 3 values in Georgia, 2.0 ($\pm$ 0.4) times greater than in Delaware, and 1.8 ($\pm$ 0.2) times greater than in Maine. Wiegert and McGinnis (1975), Bradbury and Hofstra (1976), Kirby and Gosselink (1976), and Gallagher et al. (In press) also found that Wiegert and Evans (1964) methodology yielded results greater than other methods utilized. If Method 3 is an underestimate and Method 5 a potential overestimate, the true net aerial primary production probably lies somewhere between these values. Assuming that the tidal influence was significant in these systems, ANPP is assumed to be closer to the method devised by Wiegert and Evans (1964) even with its potential flaws. The modification utilized to produce these values for Method 5 (Part III) should have produced a reasonable estimate. It is also necessary to consider that this method (Method 5) was the only one that attempted to measure the components needed for an accurate estimate of net aerial primary production.

119. These data indicated that the method utilized for computing ANPP could significantly influence the conclusion drawn from a production study in the salt marsh ecosystem. A comparison of ANPP values for *Spartina patens* supports this conclusion. Method 1 indicated that all locations are equal in production, Method 2 indicated that Maine was the most productive followed by Georgia; Method 3 indicated results identical to Method 2; Method 4 indicated Maine was the most productive followed by Delaware; and Method 5 again indicated a Maine, Georgia, then Delaware trend of decreasing magnitude of angiosperm ANPP. Species morphology, location, and general environment may also significantly affect the outcome of any single method as has already been indicated.

120. The methodology of Smalley (1958) and that of Wiegert and Evans (1964) allude to ANPP estimates applicable to the salt marsh system. Smalley's method results in underestimates of ANPP, while Wiegert and Evans' estimates are potentially inflated. Therefore, the

estimated annual net aerial primary production, as stated earlier, is an intermediate value. It appears feasible that the two values be averaged for the best ANPP estimate for these plant species and the resultant estimates are found in Figure 21.

121. The generally higher turnover rates (Table 14) observed in Maine appear to be the result of increased tidal influence on these plants (Part III). This influence tended to inflate the Wiegert and Evans (1964) ANPP values to a greater degree in Maine than in Delaware and Georgia where tidal influence was potentially less (Part III). The low turnover found in the Georgia *Borrichia frutescens* was a result of its woody nature. The exceptionally high turnover of Georgia *Distichlis spicata* stresses the potential importance of production determination methodology. A brief assessment of peak living biomass values, or even the changes in living biomass without a more in-depth consideration of the additional components effectively influencing production, could be extremely misleading.

122. In this report, less emphasis is being placed on production determination because of the multitude of publications already in existence. However, no single method devised to date adequately evaluates net primary production in salt marsh ecosystems. Conversion of one method to another through statistical evaluations of present data is a feasible approach, although these data indicate a tendency for species to require different conversion factors when transforming estimates. This process does not appear to be one that will be completed in the near future and the accuracy of such a procedure must be considered. Standardizing methodology is an alternative that will result in comparable values; however, the conclusions drawn between species or locations may contain significant inaccuracies. Many researchers have suggested that variability can be reduced by adoption of techniques applicable to the community (Rickett 1922, Walker 1947, Brown 1954, Pearsall and Graham 1956, Edwards and Owens 1960, Westlake 1963).

123. This community approach, with considerations of species morphology and geographic location, appears at present to be neces-

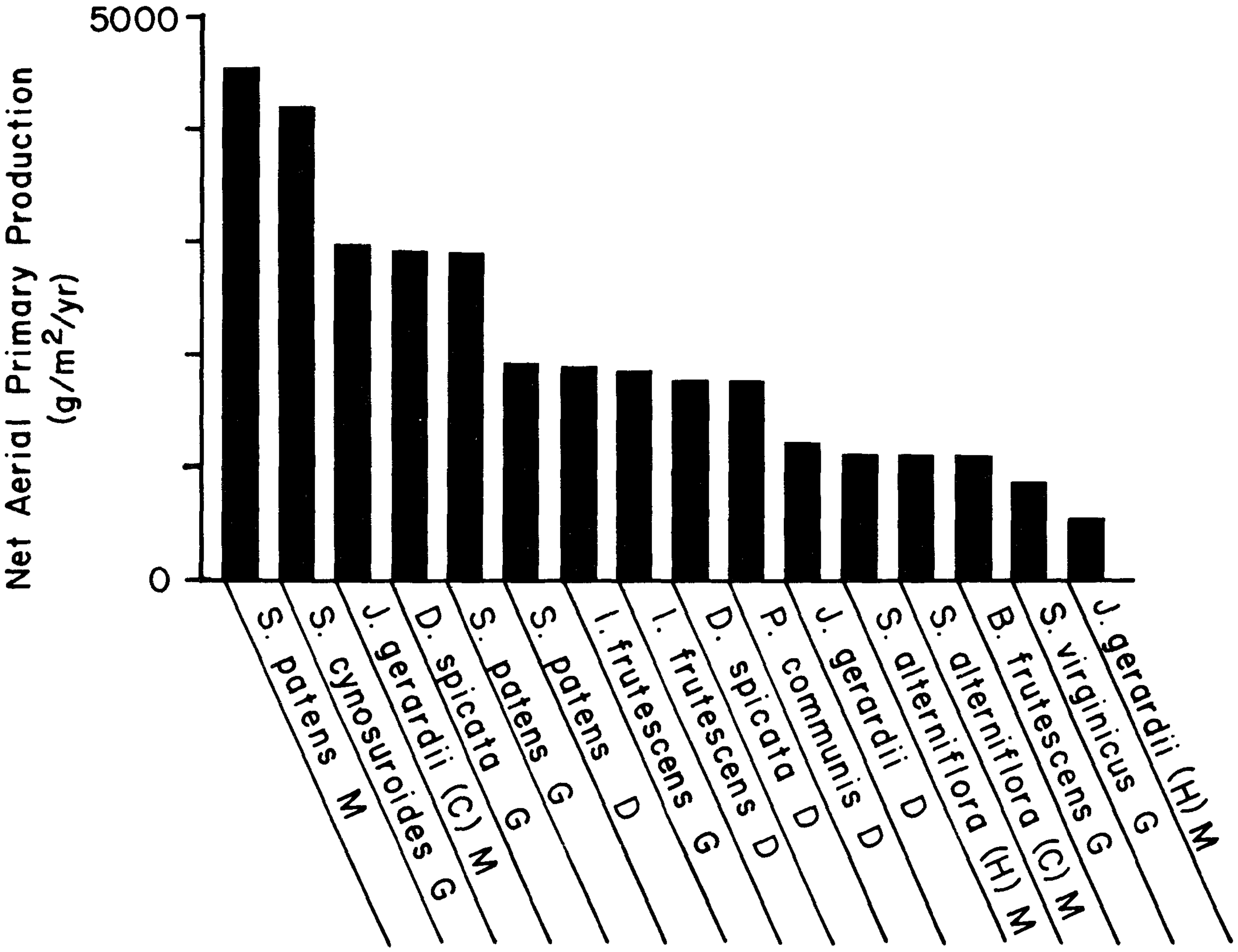


Figure 21. Estimated net aerial primary production for angiosperms sampled, based on the average value of Methods 3 and 5 (C = Creekbank, H = Highmarsh, M = Maine, D = Delaware, G = Georgia)

Table 14

Estimated Turnover Based on ANPP Estimates Resulting from Averaging Methods 3 and 5 and the Peak Standing Crop (ANPP/Method 1 Values)

Angiosperms	Estimated Turnover, $g/m^2/yr$ Maine	Delaware	Georgia
B. frutescens[a]			0.7
D. spicata		1.9	7.1
I. frutescens[a]		1.3	1.5
J. gerardii (C)[b]	4.6		
J. gerardii (H)[c]	2.4	2.3	
P. communis		1.8	
S. alterniflora (C)[b]	2.7		
S. alterniflora (H)[c]	4.8		
S. cynosuroides			2.3
S. patens	5.1	2.3	3.0
S. virginicus			3.3

[a]Smalley's ANPP estimates/method 1 values.

[b]Creekbank.

[c]Highmarsh.

sary. Such an approach also tends to rule out standardization as a viable solution and again leads one to estimation methodology, which is not comparable between, or even within, ecosystems. Therefore, if the goal of the researcher is to collect and evaluate accurate information on the primary producers, the issue of ANPP estimation methodology should not become stagnant until a means of estimating net annual primary production is devised that confidently results in reliable estimates of this parameter.

LITERATURE CITED IN PART IV

Bradbury, I. K. and G. Hofstra. 1976. Vegetation death and its importance in primary production measurements. Ecology 57: 209-211.

Brown, D. 1954. Methods of surveying and measuring vegetation. Bull. Bur. Past., Abeystw. No. 42. 223 p.

Edwards, R. W. and M. Owens. 1960. The effects of plants on river conditions. I. J. Ecol. 48: 151-160.

Gallagher, J. L., R. J. Reimold, R. A. Linthurst, and W. J. Pfeiffer. (In Press). Aerial Production, mortality, and mineral accumulation dynamics in *Spartina alterniflora* and *Juncus roemerianus* in a Georgia salt marsh. (Ecology)

Kennedy, R. K. 1972. Preliminary network evaluation on methods of primary producer biomass estimation. Pp. 30-46. In: P. G. Risser (Ed.), Preliminary Producer Data Synthesis. 1970 Comprehensive Sites. US/IBP Grassland Biome Tech. Rep. No. 161. Colorado State Univ., Fort Collins.

Kirby, C. J., Jr. 1971. The annual net primary production and decomposition of salt marsh grass *Spartina alterniflora* Loisel. in the Barataria Bay estuary of Louisiana. Ph.D. Thesis, Louisiana State University, Baton Rouge. 74 p.

Kirby, D. J. and J. G. Gosselink. 1976. Primary production in a Louisiana gulf coast *Spartina alterniflora* marsh. Ecology 57(5): 1052-1059.

Milner, C. and R. E. Hughes. 1968. Methods for the measurement of the primary production of grasslands. IBP Handbook No. 6, Blackwell Scientific Publ., Oxford. 70 p.

Ovington, S. C., D. Heitkamp, and D. Lawrence. 1963. Plant biomass and productivity of prairie, savanna, oakwood, and maize field ecosystems in central Minnesota. Ecology 44: 52-63.

Pearsall, W. H. and E. Graham. 1956. Production ecology. I. Oikos 7: 193-201.

Reimold, R. J., J. L. Gallagher, R. A. Linthurst, and W. J. Pfeiffer. 1975. Pp. 217-228. Detritus production in coastal Georgia salt marshes. In: E. Cronin (ed.), Estuarine Research. Academic

Press, Inc., New York. Vol. II.

Rickett, H. W. 1922. A quantitative study of the larger aquatic plants of Lake Mendota, Wisconsin. Trans. Wis. Acad. Sci. Arts Lett. 20: 501-527.

Singh, J. S. and P. S. Yadava. 1972. Biomass structure and net primary productivity in the grassland ecosystem at Kuruleshetra. pp. 59-74. In: Golley, P. M. and F. B. Golley (eds.), Papers from a Symposium on Tropical Ecology with Emphasis on Organic Productivity. University of Georgia Press, Athens.

Singh, J. S. and P. S. Yadava. 1974. Seasonal variation in composition, plant biomass, and net primary productivity of a tropical grassland at Kurukshetra, India. Ecol. Monogr. 44: 351-376.

Singh, J. S., W. K. Lauenroth, and R. K. Steinhorst. 1975. Review and assessment of various techniques for estimating net aerial primary production in grasslands from harvest data. Bot. Rev. 41(2): 181-232.

Smalley, A. E. 1958. The role of two invertebrate populations, *Littorina irrorata* and *Orchelimum fidicinum* in the energy flow of a salt marsh ecosystem. Ph.D. Thesis. University of Georgia, Athens. 126 pp.

Valiela, I., J. M. Teal and W. J. Sass. 1975. Production and dynamics of salt marsh vegetation and the effect of experimental treatment with sewage sludge. J. Appl. Ecol. 12(3): 973-981.

Walker, F. T. 1947. Sublittoral seaweed survey. J. Ecol. 35: 166-185.

Westlake, D. F. 1963. Comparisons of plant productivity. Biol. Rev. 38: 385-425.

Wiegert, R. and F. C. Evans. 1964. Primary production and the disappearance of dead vegetation on an old field in Southeastern Michigan. Ecology 45(1): 49-63.

Wiegert, R. G. and J. T. McGinnis. 1975. Annual production and disappearance of detritus on three South Carolina old fields. Ecology 56: 129-140.

DREDGED MATERIAL RESEARCH PROGRAM

TECHNICAL REPORT D-77-36

PRIMARY PRODUCTIVITY OF MINOR MARSH PLANTS IN DELAWARE, GEORGIA, AND MAINE

by

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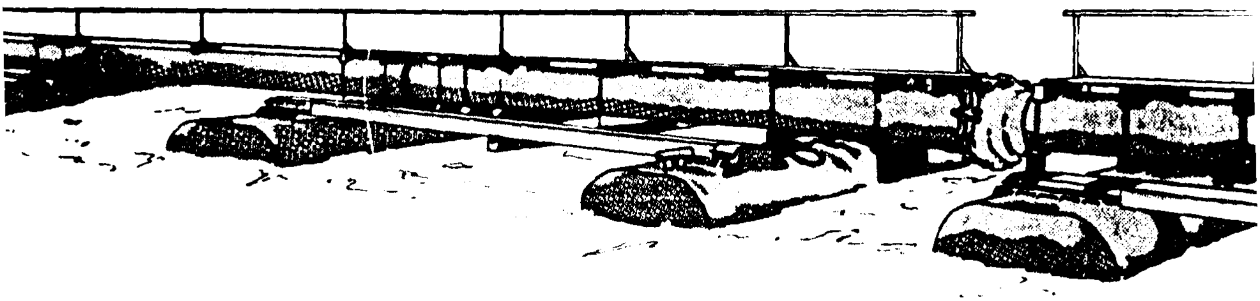

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Monitored by Environmental Effects Laboratory
U. S. Army Engineer Waterways Experiment Station
P. O. Box 631, Vicksburg, Miss. 39180

APPENDIX A: MONTHLY CLIMATOLOGICAL DATA FOR SAMPLE FROM NOAA

Month	Daily Mean °C	Daily Mean °F	Mean Maximum °C	Mean Maximum °F	Mean Minimum °C	Mean Minimum °F	Rainfall in.	Rainfall cm
				Bar Harbor, Maine				
August 1973	20.8	(69.4)	26.5	(79.7)	15.0	(59.0)	2.91	(7.39)
September	15.0	(59.0)	20.5	(68.9)	9.5	(49.1)	3.80	(9.65)
October	9.9	(49.8)	14.2	(57.6)	5.6	(42.0)	4.77	(12.12)
November	3.4	(38.2)	7.3	(45.1)	.4	(31.2)	3.18	(8.08)
December	1.2	(34.2)	5.8	(42.4)	-3.3	(26.0)	8.56	(21.74)
January 1974	-4.4	(24.0)	0.2	(32.3)	-9.1	(15.7)	3.07	(7.80)
February	-5.3	(22.5)	-0.4	(31.3)	-10.2	(13.7)	5.18	(13.16)
March	0.3	(32.5)	5.1	(41.1)	-4.6	(23.8)	4.89	(12.42)
April	7.8	(46.0)	13.6	(56.5)	1.9	(35.4)	3.90	(9.91)
May	10.1	(50.1)	15.4	(59.8)	4.6	(40.3)	4.04	(10.26)
June	16.9	(62.5)	23.6	(74.5)	10.3	(50.5)	2.90	(7.37)
July	19.2	(66.6)	25.6	(78.0)	12.8	(55.1)	2.04	(5.18)
August	20.6	(69.1)	27.4	(81.3)	13.8	(56.8)	2.02	(5.13)
September	14.7	(58.5)	19.5	(67.1)	9.9	(49.9)	8.71	(22.12)
October	7.4	(45.4)	10.2	(54.0)	2.7	(36.8)	1.22	(3.10)
November	4.3	(39.7)	8.1	(46.5)	0.4	(32.8)	4.50	(11.43)
December	-0.5	(31.1)	3.4	(38.1)	-4.4	(24.0)	2.72	(16.91)
January 1975	-3.4	(25.9)	1.3	(34.3)	-8.1	(17.4)	5.19	(13.18)
February	-4.2	(24.4)	-0.3	(31.5)	-8.3	(17.3)	1.82	(4.62)
March	0.3	(32.5)	4.4	(40.4)	-4.2	(24.5)	4.52	(11.48)
April	5.6	(42.1)	11.3	(52.3)	-0.1	(31.8)	3.54	(8.9[illegible]
May	13.5	(56.3)	19.7	(67.5)	7.3	(45.1)	2.35	(5.97)
June	17.5	(63.5)	23.8	(74.9)	11.1	(52.0)	6.42	(16.31)
July	20.9	(69.5)	26.8	(80.3)	14.9	(58.9)	2.40	(6.10)
August	19.8	(67.6)	26.1	(78.9)	13.5	(56.3)	6.76	(2.66)
				Lewes, Delaware				
August 1973	24.3	(75.7)	28.9	(84.1)	19.6	(67.2)	26.34	(10.37)
September	21.1	(70.0)	26.0	(78.8)	16.2	(61.1)	6.88	(2.71)
October	15.1	(59.1)	20.9	(69.7)	9.2	(48.5)	4.24	(1.67)
November	9.7	(49.4)	15.2	(59.3)	4.2	(39.5)	4.57	(1.80)
December	5.2	(41.4)	10.2	(50.4)	0.2	(32.4)	16.84	(6.63)
January 1974	5.1	(41.1)	9.6	(49.3)	0.4	(32.8)	6.02	(2.37)
February	2.2	(35.9)	7.1	(44.8)	-2.8	(27.0)	5.69	(2.24)
March	7.4	(45.4)	12.4	(54.3)	2.5	(36.5)	11.20	(4.41)
April	13.6	(56.4)	19.8	(67.7)	7.3	(45.1)	4.65	(1.83)
May	16.7	(62.0)	22.0	(71.6)	11.3	(52.4)	13.84	(5.45)
June	20.3	(68.6)	24.7	(76.4)	15.9	(60.7)	15.32	(6.03)
July	24.0	(75.2)	29.4	(84.9)	18.6	(65.4)	1.65	(0.65)
August	23.6	(74.4)	28.0	(82.4)	19.1	(66.4)	15.14	(5.96)
September	20.2	(68.3)	25.1	(77.1)	15.3	(59.5)	5.92	(2.33)
October	12.7	(54.9)	18.8	(65.9)	6.6	(43.8)	6.50	(2.56)
November	8.9	(48.1)	14.4	(58.0)	3.4	(38.1)	2.21	(0.87)
December	4.9	(40.8)	9.4	(49.0)	0.3	(32.5)	12.12	(4.77)
January 1975	4.3	(39.8)	9.4	(48.9)	-0.7	(30.7)	13.51	(5.32)

(continued)

Month	Daily Mean °C	Daily Mean °F	Mean Maximum °C	Mean Maximum °F	Mean Minimum °C	Mean Minimum °F	Rainfall in.	Rainfall cm
			Lewes, Delaware					
February 1975	3.9	(39.1)	8.5	(47.3)	-0.7	(30.8)	8.64	(3.40)
March	6.1	(42.9)	10.9	(51.7)	1.2	(34.1)	11.89	(4.68)
April	9.1	(48.4)	14.3	(57.8)	3.8	(38.9)	14.00	(5.51)
May	17.6	(63.6)	22.4	(72.4)	12.7	(54.8)	9.88	(3.89)
June	21.6	(70.8)	26.1	(78.9)	17.0	(62.6)	8.20	(3.23)
July	23.6	(74.4)	28.2	(82.8)	18.9	(66.0)	17.75	(6.99)
August	24.5	(76.1)	29.8	(85.6)	19.2	(66.5)	14.88	(5.86)
			Sapelo Island, Georgia					
August 1973	26.3	(79.4)	30.6	(87.0)	22.1	(71.7)	22.02	(8.67)
September	26.2	(79.1)	30.1	(86.1)	22.2	(72.0)	23.34	(9.19)
October	21.6	(70.9)	26.8	(80.2)	16.4	(61.5)	7.77	(3.06)
November	17.8	(64.0)	24.2	(75.6)	11.3	(52.3)	3.20	(1.26)
December	11.1	(52.0)	17.0	(62.6)	5.2	(41.4)	15.19	(5.98)
January 1974	18.1	(64.5)	23.6	(74.5)	12.5	(54.5)	2.72	(1.07)
February	12.8	(55.0)	19.6	(67.3)	5.9	(42.6)	8.00	(3.15)
March	17.8	(64.1)	24.4	(75.9)	11.3	(52.3)	8.46	(3.33)
April	19.2	(66.5)	25.1	(77.2)	13.2	(55.8)	4.06	(1.60)
May	23.9	(75.0)	28.8	(83.9)	18.9	(66.0)	3.51	(1.38)
June	24.8	(76.6)	29.7	(85.4)	19.9	(67.8)	17.32	(6.82)
July	26.2	(79.1)	30.8	(86.8)	21.6	(70.8)	19.18	(7.55)
August	26.2	(79.1)	30.4	(86.8)	21.9	(71.4)	24.00	(9.45)
September	25.0	(77.0)	29.3	(84.7)	20.7	(69.3)	36.30	(14.29)
October	18.8	(65.8)	24.3	(75.7)	13.3	(55.9)	1.57	(0.62)
November	15.8	(60.5)	21.7	(71.1)	9.9	(49.9)	2.18	(0.86)
December	11.7	(53.1)	17.1	(62.8)	6.3	(43.3)	6.10	(2.40)
January 1975	13.2	(55.7)	19.1	(66.4)	7.2	(45.0)	8.92	(3.51)
February	13.9	(57.1)	19.5	(67.1)	8.3	(47.0)	7.65	(3.01)
March	15.2	(59.3)	21.3	(70.4)	8.9	(48.1)	9.05	(3.17)
April	18.2	(64.8)	24.0	(75.2)	12.4	(54.4)	10.13	(3.99)
May	23.4	(74.1)	28.4	(83.1)	18.3	(65.0)	10.72	(4.22)
June	25.9	(78.6)	30.9	(87.6)	20.8	(69.5)	5.72	(2.25)
July	26.1	(79.0)	30.7	(87.3)	21.5	(70.7)	10.70	(8.16)
August	26.9	(80.4)	31.8	(89.3)	21.9	(71.5)	9.04	(3.56)

APPENDIX B: TIDAL DATA FOR THE COLLECTION SITES

Month	Mean Low Water m	Mean Low Water ft	Mean High Water m	Mean High Water ft	Maximum High Water m	Maximum High Water ft
			Bar Harbor, Maine			
August 1973	-0.01	(-0.02)	2.83	(9.29)	3.31	(10.86)
September	0.04	(0.12)	2.81	(9.21)	3.25	(10.66)
October	0.07	(0.23)	2.77	(9.08)	3.28	(10.75)
November	-0.04	(-0.13)	2.70	(8.87)	3.27	(10.74)
December	-0.04	(-0.14)	2.71	(8.89)	3.55	(11.66)
January 1974	-0.20	(-0.66)	2.58	(8.48)	3.36	(11.03)
February	-0.22	(-0.71)	2.55	(8.38)	3.45	(11.31)
March	-0.24	(-0.78)	2.49	(8.18)	3.16	(10.37)
April	-0.15	(-0.50)	2.56	(8.40)	3.16	(10.36)
May	-0.18	(-0.59)	2.65	(8.70)	3.01	(9.86)
June	-0.17	(-0.57)	2.67	(8.75)	3.42	(11.21)
July	-0.13	(-0.42)	2.68	(8.75)	3.31	(10.86)
August	-0.20	(-0.64)	2.57	(8.43)	3.29	(10.78)
September	-0.05	(-0.17)	2.74	(9.00)	3.37	(11.05)
October	-0.06	(-0.20)	2.69	(8.81)	3.30	(10.82)
November	-0.18	(-0.60)	2.62	(8.59)	3.36	(11.01)
December	-0.07	(-0.22)	2.80	(9.08)	3.65	(11.98)
January 1975	-0.09	(-0.30)	2.77	(9.09)	3.52	(11.54)
February	-0.05	(-0.17)	2.75	(9.02)	3.56	(11.69)
March	-0.06	(-0.19)	2.82	(9.24)	3.45	(11.33)
April	-0.03	(-0.09)	2.82	(9.25)	3.41	(11.20)
May	0.00	(0.00)	2.79	(9.16)	3.31	(10.87)
June	0.04	(0.13)	2.82	(9.25)	3.23	(10.61)
July	0.03	(0.10)	2.80	(9.13)	3.36	(11.04)
August	0.03	(0.10)	2.81	(9.21)	3.42	(11.22)
			Lewes, Delaware			
August 1973	0.19	(0.61)	1.46	(4.78)	1.88	(6.16)
September	0.22	(0.73)	1.47	(4.81)	2.07	(6.76)
October	0.14	(0.47)	1.41	(4.63)	2.12	(6.96)
November	0.01	(0.02)	1.25	(4.09)	1.79	(5.86)
December	0.05	(0.17)	1.25	(4.14)	2.30	(7.56)
January 1974	0.09	(0.28)	1.31	(4.29)	1.90	(6.23)
February	0.05	(0.18)	1.32	(4.32)	1.96	(6.43)
March	-0.02	(-0.08)	1.23	(4.03)	1.77	(5.80)
April	-0.04	(-0.13)	1.25	(4.13)	1.73	(5.68)
May	0.07	(0.23)	1.35	(4.43)	1.79	(5.86)
June	0.16	(0.51)	1.42	(4.66)	1.98	(6.50)
NOAA tide gauge was destroyed in a fire. Data are unavailable from July 1974 through December 1974.						
January 1975	0.02	(0.06)	1.26	(4.14)	1.57	(5.16)
February	0.00	(0.00)	1.29	(4.22)	1.01	(5.95)
March	0.02	(0.06)	1.27	(4.18)	1.41	(4.62)

(continued)

Month	Mean Low Water m	ft	Mean High Water m	ft	Maximum High Water m	ft
			Lewes, Delaware			
April 1975	0.08	(0.27)	1.36	(4.47)	1.91	(6.28)
May	0.08	(0.27)	1.36	(4.47)	1.83	(5.99)
June	0.07	(0.22)	1.35	(4.42)	1.91	(6.26)
July	0.12	(0.39)	1.39	(4.56)	1.81	(5.93)
			Fort Pulaski, Georgia			
August 1973	0.16	(0.53)	2.24	(7.35)	2.70	(8.86)
September	0.31	(1.01)	2.33	(7.64)	2.90	(9.51)
October	0.42	(1.39)	2.37	(7.79)	2.82	(9.25)
November	0.29	(0.94)	2.31	(7.58)	2.97	(9.75)
December	0.07	(0.22)	2.12	(6.94)	2.74	(8.99)
NOAA tide data unavailable January 1974 through December 1974.						
January 1975	-0.03	(-0.10)	2.03	(6.66)	2.59	(8.50)
February	0.05	(-0.16)	2.13	(6.99)	2.59	(8.50)
March	-0.02	(0.08)	2.07	(6.78)	2.59	(8.50)
April	0.05	(0.15)	2.10	(6.89)	2.53	(8.30)
May	0.13	(0.44)	2.18	(7.15)	2.53	(8.30)
June	0.14	(0.46)	2.32	(7.60)	2.65	(8.70)
July	0.03	(0.09)	2.05	(6.73)	2.47	(8.10)
August	0.05	(0.16)	2.11	(6.91)	2.50	(8.20)

APPENDIX C: MONTHLY MEAN VALUES FOR LIVING AERIAL BIOMASS, DEAD AERIAL BIOMASS, LIVE TO DEAD RATIOS, LIVING STEM DENSITIES, AND INDIVIDUAL LIVING STEM WEIGHTS, FOR THE ANGIOSPERMS SAMPLED. (LIVING STEM WEIGHTS ARE BASED ONLY ON PLOTS THAT HAD LIVING MATERIAL PRESENT.)

Collection Date	L	D	L:D	SD	LSW
		Borrichia frutescens, Georgia			
27 August 1973	1700.4 ± 697.1	270.8 ± 64.5	8.5 ± 3.5	278.0 ± 16.6	7.0 ± 3.5
22 October 1973	648.3 ± 15.0	191.0 ± 25.9	3.7 ± 0.5	298.4 ± 51.2	2.7 ± 0.6
17 December 1973	882.4 ± 24.6	221.0 ± 36.8	4.9 ± 0.2	213.2 ± 12.0	4.2 ± 0.2
11 February 1974	791.8 ± 49.5	187.2 ± 23.9	4.4 ± 0.4	297.2 ± 23.0	2.7 ± 0.1
8 April 1974	850.8 ± 63.7	291.1 ± 36.2	3.1 ± 0.3	372.8 ± 15.6	2.3 ± 0.2
3 June 1974	1860.1 ± 122.0	278.4 ± 21.4	6.7 ± 0.4	322.0 ± 42.5	6.6 ± 1.6
29 July 1974	1267.4 ± 152.4	208.8 ± 33.8	6.3 ± 0.5	242.8 ± 43.8	6.2 ± 1.5
24 September 1974	763.6 ± 47.8	208.6 ± 25.4	4.0 ± 0.7	247.8 ± 28.0	3.2 ± 0.3
18 November 1974	1090.3 ± 124.7	190.4 ± 26.8	6.4 ± 1.1	309.6 ± 11.3	3.5 ± 0.4
13 January 1975	841.0 ± 54.7	237.7 ± 29.6	3.8 ± 0.5	264.0 ± 29.8	3.4 ± 0.5
11 March 1975	1031.0 ± 53.7	183.6 ± 14.3	5.7 ± 0.4	329.2 ± 32.7	3.3 ± 0.5
5 May 1975	979.6 ± 106.8	196.8 ± 37.4	5.4 ± 0.8	380.4 ± 27.4	2.6 ± 0.3
30 June 1975	1251.0 ± 113.6	210.8 ± 46.4	10.4 ± 5.6	323.2 ± 5.4	0.2 ± 0.1
25 August 1975	1240.2 ± 22.0	211.0 ± 27.7	6.0 ± 0.8	293.2 ± 18.9	0.2 ± 0.0

NOTE: Monthly mean values, L = living material, g/m^2; D = dead material, g/m^2; L:D = ratio of live to dead; SD = living stem densities, stems/m^2; and LSW = individual living stem weights, g/plant.

Collection Date	L	D	L:D	SD	LSW
Distichlis spicata, Delaware					
27 August 1973	459.8 ± 29.9	248.2 ± 67.8	3.3 ± 1.5	3130.0 ± 362.2	0.2 ± 0.0
22 October 1973	316.0 ± 47.5	748.0 ± 132.7	0.5 ± 0.1	2300.0 ± 291.6	0.1 ± 0.0
17 December 1973	0.0 ± 0.0	872.0 ± 79.1	0.0 ± 0.0	700.0 ± 94.9	0.0 ± 0.0
11 February 1974	2.0 ± 2.0	1302.0 ± 178.6	0.0 ± 0.0	20.0 ± 20.0	0.1 ± 0.0
8 April 1974	4.0 ± 4.0	1188.0 ± 137.0	0.0 ± 0.0	420.0 ± 162.5	0.0 ± 0.0
3 June 1974	282.0 ± 32.9	602.0 ± 65.2	0.5 ± 0.1	4280.0 ± 554.4	0.6 ± 0.0
29 July 1974	570.0 ± 45.4	578.0 ± 70.3	1.1 ± 0.2	4080.0 ± 495.4	0.1 ± 0.0
24 September 1974	1142.0 ± 398.0	554.0 ± 112.6	2.3 ± 0.6	2980.0 ± 535.2	0.4 ± 0.1
18 November 1974	66.0 ± 25.8	912.0 ± 79.2	0.1 ± 0.0	660.0 ± 186.0	0.1 ± 0.0
13 January 1975	10.0 ± 4.5	102.0 ± 209.4	0.0 ± 0.0	220.0 ± 111.4	0.0 ± 0.0
11 March 1975	0.0 ± 0.0	894.0 ± 146.9	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
5 May 1975	64.0 ± 11.2	552.0 ± 118.9	0.1 ± 0.0	4660.0 ± 832.8	0.0 ± 0.0
30 June 1975	586.0 ± 51.1	334.0 ± 61.1	2.1 ± 0.6	6160.0 ± 629.8	0.1 ± 0.0
25 August 1975	572.0 ± 89.6	302.0 ± 29.6	1.9 ± 0.3	5100.0 ± 782.9	0.1 ± 0.0

Collection Date	L	D	L:D	SD	LSW
		Distichlis spicata, Georgia			
27 August 1973	278.2 ± 15.1	331.2 ± 63.6	1.0 ± 0.2	1140.0 ± 237.5	0.3 ± 0.1
22 October 1973	22.8 ± 19.9	764.6 ± 68.0	0.3 ± 0.0	1222.0 ± 155.7	0.2 ± 0.0
17 December 1973	132.4 ± 19.4	493.4 ±134.7	0.3 ± 0.0	942.0 ± 86.4	0.1 ± 0.0
11 February 1974	128.0 ± 11.6	1132.0 ±168.1	0.1 ± 0.0	1380.0 ± 97.0	0.0 ± 0.0
8 April 1974	282.0 ± 55.9	794.0 ±135.9	0.4 ± 0.1	1560.0 ± 172.0	0.2 ± 0.0
3 June 1974	206.0 ± 43.8	920.0 ±335.8	0.3 ± 0.1	2300.0 ± 700.0	0.1 ± 0.0
29 July 1974	338.0 ± 70.4	838.0 ±180.9	0.4 ± 0.1	1940.0 ± 460.0	0.2 ± 0.0
24 September 1974	458.0 ± 46.8	612.0 ±218.9	1.6 ± 0.8	1980.0 ± 196.0	0.2 ± 0.0
18 November 1974	438.0 ± 91.7	1260.0 ±284.6	0.4 ± 0.1	1240.0 ± 166.1	0.1 ± 0.0
13 January 1975	192.0 ± 66.4	804.0 ±101.4	0.2 ± 0.1	1240.0 ± 166.1	0.1 ± 0.0
11 March 1975	154.0 ± 39.8	930.0 ± 83.4	0.2 ± 0.1	1100.0 ± 228.0	0.1 ± 0.0
5 May 1975	138.0 ± 15.0	6800.0 ±113.1	0.2 ± 0.1	1100.0 ± 228.0	0.1 ± 0.0
30 June 1975	288.0 ± 79.3	764.0 ±115.6	0.4 ± 0.1	1540.0 ± 372.3	0.2 ± 0.0
25 August 1975	298.0 ± 50.4	852.0 ±132.2	0.4 ± 0.1	1640.0 ± 397.0	0.2 ± 0.0

Collection Date	L	D	L:D	SD	LSW
		Iva frutescens, Delaware			
27 August 1973	716.6 ± 359.8	237.8 ± 225.8	1.2 ± 0.8	57.6 ± 21.1	28.2 ± 14.8
22 October 1973	1253.4 ± 187.6	106.8 ± 61.4	33.6 ± 13.2	93.2 ± 24.9	18.0 ± 5.4
17 December 1973	775.0 ± 140.6	234.5 ± 97.4	6.0 ± 2.0	47.2 ± 8.6	23.9 ± 10.5
11 February 1974	427.2 ± 116.5	150.2 ± 91.9	5.1 ± 1.0	25.2 ± 7.9	22.0 ± 7.6
8 April 1974	977.6 ± 228.3	424.1 ± 50.1	2.6 ± 0.7	39.2 ± 4.8	25.8 ± 6.8
3 June 1974	1073.2 ± 189.3	447.2 ± 143.3	3.0 ± 0.7	62.4 ± 11.1	17.5 ± 1.2
29 July 1974	701.2 ± 164.7	203.9 ± 91.2	5.8 ± 1.8	35.2 ± 6.2	20.5 ± 3.0
24 September 1974	1580.2 ± 129.2	522.6 ± 153.6	4.2 ± 1.1	36.8 ± 3.4	45.2 ± 6.7
18 November 1974	1491.4 ± 380.4	565.5 ± 215.5	3.8 ± 1.2	46.0 ± 14.8	48.3 ± 14.5
13 January 1975	768.1 ± 250.2	451.0 ± 100.0	2.5 ± 1.0	43.2 ± 7.7	18.5 ± 4.8
11 March 1975	853.6 ± 64.0	309.8 ± 82.5	4.2 ± 1.6	41.2 ± 10.8	28.1 ± 9.5
5 May 1975	606.1 ± 55.5	128.3 ± 46.6	6.8 ± 2.3	18.4 ± 5.4	50.7 ± 16.5
30 June 1975	1097.0 ± 229.4	320.9 ± 157.7	5.4 ± 1.2	39.2 ± 9.5	34.6 ± 8.4
25 August 1975	966.8 ± 360.4	166.3 ± 44.0	5.5 ± 1.2	14.4 ± 3.6	54.1 ± 13.6

Collection Date	L	D	L:D	SD	LSW
		Iva frutescens, Georgia			
27 August 1973	- -	- -	- -	- -	- -
22 October 1973	- -	- -	- -	- -	- -
17 December 1973	- -	- -	- -	- -	- -
11 February 1974	344.2 ± 185.8	900.6 ± 85.7	0.4 ± 0.2	12.0 ± 4.6	23.1 ± 10.4
8 April 1974	396.8 ± 117.6	1017.6 ± 340.0	0.5 ± 0.1	14.4 ± 2.6	27.8 ± 5.6
3 June 1974	1166.3 ± 595.3	652.9 ± 212.8	1.9 ± 0.6	25.2 ± 3.2	42.5 ± 16.3
29 July 1974	1227.0 ± 336.3	1360.6 ± 299.0	1.3 ± 0.5	15.6 ± 4.0	99.3 ± 36.1
24 September 1974	1181.2 ± 339.0	1194.6 ± 363.8	1.2 ± 0.3	20.8 ± 7.9	68.0 ± 20.0
18 November 1974	526.0 ± 214.1	779.8 ± 340.9	0.7 ± 0.2	11.6 ± 4.3	47.6 ± 9.0
13 January 1975	116.4 ± 55.6	945.3 ± 229.4	0.1 ± 0.1	4.8 ± 2.3	29.1 ± 8.0
11 March 1975	203.3 ± 84.3	825.1 ± 223.0	0.2 ± 0.1	5.2 ± 1.9	38.7 ± 13.2
5 May 1975	246.1 ± 114.7	538.0 ± 55.6	0.4 ± 0.2	14.0 ± 5.3	25.7 ± 14.4
30 June 1975	864.7 ± 344.1	1150.4 ± 296.2	0.8 ± 0.2	19.2 ± 3.6	43.0 ± 11.3
25 August 1975	1288.4 ± 365.1	1396.4 ± 306.8	1.1 ± 0.4	11.6 ± 1.5	107.2 ± 23.9

L

Collection Date	L	D	L:D	SD	LSW
		Juncus gerardii, Delaware			
27 August 1973	180.0 ± 29.8	454.0 ± 138.4	0.3 ± 0.1	5880.0 ± 363.9	0.0 ± 0.0
22 October 1973	0.0 ± 0.0	412.0 ± 80.5	0.0 ± 0.0	40.0 ± 40.0	0.0 ± 0.0
17 December 1973	0.0 ± 0.0	576.0 ± 71.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
11 February 1974	12.5 ± 2.2	600.0 ± 76.4	0.0 ± 0.0	1580.0 ± 139.3	0.0 ± 0.0
8 April 1974	154.0 ± 22.7	204.0 ± 29.4	0.9 ± 0.3	7240.0 ± 454.5	0.0 ± 0.0
3 June 1974	488.0 ± 44.9	324.0 ± 73.1	1.9 ± 0.5	7320.0 ± 693.8	0.1 ± 0.0
29 July 1974	268.0 ± 16.8	748.0 ± 72.7	0.4 ± 0.0	6620.0 ± 428.2	0.0 ± 0.0
24 September 1974	30.0 ± 14.5	586.0 ± 91.5	0.0 ± 0.0	1660.0 ± 244.1	0.0 ± 0.0
18 November 1974	0.0 ± 0.0	502.0 ± 78.1	0.0 ± 0.0	40.0 ± 24.5	0.0 ± 0.0
13 January 1975	8.0 ± 1.2	600.0 ± 148.0	0.0 ± 0.0	1180.0 ± 342.6	0.0 ± 0.0
11 March 1975	20.0 ± 0.0	482.0 ± 40.8	0.0 ± 0.0	2420.0 ± 235.4	0.0 ± 0.0
5 May 1975	296.0 ± 19.4	254.0 ± 23.5	1.2 ± 0.1	8840.0 ± 930.4	0.0 ± 0.0
30 June 1975	560.0 ± 79.5	182.0 ± 33.4	3.8 ± 1.2	7200.0 ± 665.6	0.1 ± 0.0
25 August 1975	310.0 ± 189.8	542.0 ± 39.2	0.5 ± 0.3	1880.0 ± 507.4	0.2 ± 0.0

Collection Date	L	D	L:D	SD	LSW
		Juncus gerardii creekbank, Maine			
3 June 1974	392.0 ± 49.3	34.0 ± 18.9	17.1 ± 11.6	8020.0 ± 773.7	0.0 ± 0.0
29 July 1974	644.0 ± 92.2	1050.0 ± 197.3	0.7 ± 0.1	7680.0 ± 511.3	0.1 ± 0.0
24 September 1974	10.0 ± 6.3	806.0 ± 115.5	0.0 ± 0.0	380.0 ± 139.3	0.0 ± 0.0
7 April 1975	14.0 ± 4.0	474.0 ± 48.9	0.0 ± 0.0	1340.0 ± 218.2	0.0 ± 0.0
5 May 1975	52.0 ± 6.6	556.0 ± 65.9	0.1 ± 0.0	7540.0 ± 610.8	0.0 ± 0.0
30 June 1975	624.0 ± 21.8	52.0 ± 13.6	15.2 ± 3.1	8680.0 ± 683.7	0.1 ± 0.0
25 August 1975	196.0 ± 100.0	412.0 ± 115.8	0.8 ± 0.6	2780.0 ±1063.7	0.1 ± 0.0
		Juncus gerardii highmarsh, Maine			
3 June 1974	- -	- -	- -	- -	- -
29 July 1974	244.0 ± 56.1	46.0 ± .8	8.0 ± 2.0	3340.0 ± 294.3	0.1 ± 0.0
24 September 1974	82.0 ± 24.0	432.0 ± 34.4	0.2 ± 0.0	2460.0 ± 292.6	0.0 ± 0.0
7 April 1975	0.0 ± 0.0	51.0 ± 7.1	0.0 ± 0.0	800.0 ± 200.0	0.0 ± 0.0
5 May 1975	0.6 ± 0.2	55.6 ± 6.6	0.0 ± 0.0	122.0 ± 20.8	0.0 ± 0.0
30 June 1975	27.0 ± 3.9	22.0 ± 2.1	1.2 ± 0.2	288.0 ± 26.9	0.1 ± 0.0
25 August 1975	230.0 ± 32.6	74.0 ± 8.1	3.1 ± 0.3	3880.0 ± 239.6	0.1 ± 0.0

Collection Date	L	D	L:D	SD	LSW
		Phragmites communis, Delaware			
27 August 1973	1379.6 ± 149.8	135.6 ± 25.3	11.6 ± 2.3	84.4 ± 9.1	16.7 ± 1.8
22 October 1973	657.1 ± 96.8	386.4 ± 80.0	2.1 ± 0.7	39.4 ± 4.9	16.6 ± 1.0
17 December 1973	0.0 ± 0.0	4158.4 ± 214.7	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
11 February 1974	0.0 ± 0.0	4695.2 ± 601.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
8 April 1974	2.6 ± 1.2	3050.7 ± 278.7	0.0 ± 0.0	15.6 ± 6.5	0.1 ± 0.0
3 June 1974	234.8 ± 60.7	1648.4 ± 358.3	0.1 ± 0.0	65.6 ± 9.4	3.4 ± 0.9
29 July 1974	965.6 ± 96.4	2203.6 ± 204.7	0.4 ± 0.0	68.8 ± 7.1	14.1 ± 0.4
24 September 1974	835.2 ± 101.9	2294.2 ± 189.9	0.4 ± 0.0	57.2 ± 8.8	15.3 ± 1.6
18 November 1974	4.3 ± 3.4	2453.3 ± 443.8	0.0 ± 0.0	1.2 ± 0.8	3.1 ± 1.9
13 January 1975	0.0 ± 0.0	3354.0 ± 297.4	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
11 March 1975	0.0 ± 0.0	2319.3 ± 234.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
5 May 1975	23.6 ± 12.4	3723.7 ± 367.4	0.0 ± 0.0	31.6 ± 15.6	0.7 ± 0.1
30 June 1975	875.4 ± 92.6	1464.8 ± 124.6	0.6 ± 0.1	93.2 ± 8.3	9.6 ± 1.1
25 August 1975	850.6 ± 103.1	2409.2 ± 214.3	0.4 ± 0.0	63.6 ± 5.1	13.4 ± 5.6

Collection Date	L	D	L:D	SD	LSW
		Spartina alterniflora creekbank, Maine			
3 June 1974	140.0 ± 22.7	42.8 ± 3.8	3.3 ± 0.4	3206.0 ± 663.8	0.0 ± 0.0
29 July 1974	431.2 ± 60.8	216.2 ± 52.2	2.2 ± 0.2	1956.0 ± 349.3	0.2 ± 0.0
24 September 1974	211.0 ± 15.2	431.8 ± 79.1	0.6 ± 0.1	842.0 ± 181.0	0.3 ± 0.1
7 April 1975	0.0 ± 0.0	43.4 ± 6.4	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
5 May 1975	14.2 ± 6.4	20.0 ± 5.9	0.8 ± 0.2	1196.0 ± 229.4	0.0 ± 0.0
30 June 1975	328.6 ± 4.7	45.0 ± 27.3	9.6 ± 3.1	1654.0 ± 268.1	0.2 ± 0.0
25 August 1975	369.6 ± 38.4	143.0 ± 13.0	2.6 ± 0.1	1472.0 ± 143.6	0.2 ± 0.0
		Spartina alterniflora highmarsh, Maine			
3 June 1974	73.2 ± 5.8	427.8 ± 51.1	0.1 ± 0.0	1804.0 ± 128.6	0.0 ± 0.0
29 July 1974	245.6 ± 22.5	366.0 ± 82.2	0.8 ± 0.2	826.0 ± 98.4	0.3 ± 0.1
24 September 1974	133.0 ± 24.4	640.6 ± 48.8	0.2 ± 0.0	322.0 ± 53.9	0.4 ± 0.0
7 April 1975	0.0 ± 0.0	557.2 ± 120.9	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
5 May 1975	3.8 ± 1.3	584.2 ± 21.5	0.0 ± 0.0	212.0 ± 73.4	0.2 ± 0.0
30 June 1975	234.2 ± 10.4	187.2 ± 56.9	2.8 ± 1.6	1188.0 ± 78.8	0.2 ± 0.0
25 August 1975	217.2 ± 15.1	244.2 ± 30.2	0.9 ± 0.1	680.0 ± 137.3	0.4 ± 0.1

Collection Date	L	D	L:D	SD	LSW
		Spartina cynosuroides, Georgia			
27 August 1973	1560.0 ± 333.5	291.5 ± 99.4	8.0 ± 3.5	39.2 ± 6.4	38.7 ± 3.7
22 October 1973	1218.2 ± 348.3	1092.0 ± 275.8	1.7 ± 0.7	29.2 ± 10.1	51.2 ± 17.7
17 December 1973	81.2 ± 41.4	1473.3 ± 74.8	0.0 ± 0.0	9.2 ± 2.1	9.8 ± 4.2
11 February 1974	97.0 ± 13.3	1984.0 ± 232.6	0.0 ± 0.0	84.8 ± 17.8	1.2 ± 0.2
8 April 1974	384.7 ± 56.8	2284.4 ± 204.3	0.2 ± 0.0	42.0 ± 6.3	9.3 ± 0.5
3 June 1974	1464.3 ± 199.2	1295.6 ± 155.4	1.2 ± 0.3	54.8 ± 4.8	26.6 ± 2.9
29 July 1974	1642.6 ± 349.4	927.5 ± 359.4	1.3 ± 0.6	32.8 ± 8.1	52.0 ± 3.4
24 September 1974	1212.0 ± 267.9	1160.8 ± 185.9	1.0 ± 0.2	36.8 ± 4.8	31.8 ± 3.9
18 November 1974	114.4 ± 51.0	2031.2 ± 161.6	0.0 ± 0.0	4.4 ± 1.7	22.3 ± 6.4
13 January 1975	4.1 ± 1.2	2058.0 ± 226.4	0.0 ± 0.0	16.0 ± 3.9	0.2 ± 0.0
11 March 1975	167.9 ± 31.4	1176.5 ± 290.2	0.1 ± 0.0	91.6 ± 13.1	1.8 ± 0.2
5 May 1975	842.4 ± 95.8	1322.7 ± 265.7	0.8 ± C	69.6 ± 4.5	12.1 ± 1.2
30 June 1975	2176.5 ± 203.8	1194.4 ± 355.9	2.4 ± 0.5	57.6 ± 2.9	38.0 ± 3.3
25 August 1975	1362.7 ± 374.8	2583.5 ± 340.0	0.5 ± 0.1	40.0 ± 8.2	21.1 ± 13.0

Collection Date	L	D	L:D	SD	LSW
		Spartina patens, Delaware			
27 August 1973	908.0 ± 109.1	820.0 ± 181.5	1.2 ± 0.1	5900.0 ± 573.6	0.2 ± 0.0
22 October 1973	962.0 ± 145.3	500.0 ± 84.7	2.0 ± 0.2	4880.0 ± 726.2	0.2 ± 0.0
17 December 1973	0.0 ± 0.0	642.0 ± 206.5	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
11 February 1974	30.0 ± 14.5	774.0 ± 109.2	0.0 ± 0.0	900.0 ± 258.8	0.0 ± 0.0
8 April 1974	4.0 ± 4.0	530.0 ± 92.3	0.0 ± 0.0	760.0 ± 229.4	0.0 ± 0.0
3 June 1974	114.0 ± 20.4	354.0 ± 52.4	0.3 ± 0.1	1880.0 ± 174.4	0.1 ± 0.0
29 July 1974	246.0 ± 72.6	962.0 ± 116.8	0.3 ± 0.1	3180.0 ± 220.0	0.1 ± 0.0
24 September 1974	322.5 ± 94.2	800.0 ± 93.9	0.4 ± 0.0	2460.0 ± 684.6	0.1 ± 0.0
18 November 1974	120.0 ± 13.0	750.0 ± 61.6	0.2 ± 0.0	2020.0 ± 231.1	0.1 ± 0.0
13 January 1975	96.0 ± 43.0	768.0 ± 96.0	0.1 ± 0.0	1420.0 ± 320.0	0.1 ± 0.0
11 March 1975	10.0 ± 6.3	822.0 ± 176.1	0.0 ± 0.0	580.0 ± 427.1	0.0 ± 0.0
5 May 1975	120.0 ± 17.6	828.0 ± 188.0	0.2 ± 0.0	3520.0 ± 443.2	0.0 ± 0.0
30 June 1975	332.0 ± 33.7	384.0 ± 83.2	1.1 ± 0.3	4520.0 ± 507.4	0.1 ± 0.0
25 August 1975	652.0 ± 163.4	554.0 ± 166.1	1.3 ± 0.2	5580.0 ± 608.6	0.1 ± 0.0

Collection Date	L	D	L:D	SD	LSW
Spartina patens, Georgia					
27 August 1973	504.8 ± 75.6	439.0 ± 102.7	1.8 ± 0.8	1304.0 ± 183.4	0.4 ± 0.0
22 October 1973	579.6 ± 105.6	417.8 ± 31.4	1.4 ± 0.2	1966.0 ± 172.6	0.3 ± 0.1
17 December 1973	380.0 ± 43.5	669.2 ± 99.2	0.6 ± 0.1	1226.0 ± 147.6	0.3 ± 0.0
11 February 1974	916.0 ± 173.3	618.0 ± 147.0	1.7 ± 0.3	2320.0 ± 466.3	0.4 ± 0.1
4 April 1974	980.0 ± 189.9	984.0 ± 366.2	1.5 ± 0.4	2800.0 ± 327.1	0.4 ± 0.1
3 June 1974	562.0 ± 136.5	682.0 ± 158.6	1.0 ± 0.2	1820.0 ± 372.0	0.3 ± 0.1
29 July 1974	544.0 ± 65.2	584.0 ± 75.8	1.0 ± 0.2	2020.0 ± 436.4	0.3 ± 0.1
24 September 1974	400.0 ± 98.5	366.0 ± 81.0	1.2 ± 0.2	2480.0 ± 486.2	0.2 ± 0.0
18 November 1974	276.0 ± 65.6	922.0 ± 311.6	0.4 ± 0.1	1560.0 ± 238.9	0.2 ± 0.0
13 January 1975	270.0 ± 73.4	742.0 ± 179.4	0.4 ± 0.1	1660.0 ± 143.5	0.2 ± 0.0
11 March 1975	176.0 ± 36.8	236.0 ± 71.9	0.9 ± 0.2	1460.0 ± 74.8	0.1 ± 0.0
5 May 1975	426.0 ± 109.6	980.0 ± 347.6	0.5 ± 0.2	2420.0 ± 748.6	0.2 ± 0.0
30 June 1975	912.0 ± 138.0	1324.0 ± 161.2	0.7 ± 0.2	2900.0 ± 483.7	0.3 ± 0.0
25 August 1975	618.0 ± 127.7	980.0 ± 204.6	0.8 ± 0.3	2200.0 ± 301.7	0.2 ± 0.0

Collection Date	L	D	L:D	SD	LSW
		Spartina patens, Maine			
3 June 1974	64.0 ± 22.0	124.0 ± 310.0	0.0 ± 0.0	2820.0 ± 656.8	0.3 ± 0.0
29 July 1974	866.0 ± 236.6	2026.0 ± 298.9	0.5 ± 0.2	7520.0 ± 805.1	0.1 ± 0.0
24 September 1974	700.0 ± 99.4	1205.0 ± 134.2	0.6 ± 0.2	5675.0 ± 690.3	0.1 ± 0.0
7 April 1975	0.0 ± 0.0	1692.0 ± 398.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
5 May 1975	0.0 ± 0.0	1386.0 ± 489.2	0.0 ± 0.0	200.0 ± 137.8	0.0 ± 0.0
30 June 1975	522.0 ± 120.7	1014.0 ± 311.9	0.9 ± 0.4	9520.0 ±1430.5	0.1 ± 0.0
25 August 1975	912.0 ± 195.6	132.0 ± 33.4	8.2 ± 2.7	12880.0 ±2438.3	0.1 ± 0.0

Collection Date	L	D	L:D	SD	LSW
			Sporobolus virginicus, Georgia		
27 August 1973	- -	- -	- -	- -	- -
22 October 1973	- -	- -	- -	- -	- -
17 December 1973	- -	- -	- -	- -	- -
11 February 1974	70.0 ± 15.5	262.0 ± 38.8	0.2 ± 0.0	2800.0 ± 345.0	0.0 ± 0.0
8 April 1974	184.0 ± 34.9	196.0 ± 49.9	1.1 ± 0.2	3580.0 ± 465.2	0.0 ± 0.0
3 June 1974	156.0 ± 34.1	264.0 ± 51.3	0.6 ± 0.1	2920.0 ± 536.1	0.0 ± 0.0
29 July 1974	166.0 ± 39.1	140.0 ± 34.9	1.3 ± 0.2	3360.0 ± 777.6	0.0 ± 0.0
24 September 1974	262.0 ± 45.9	180.0 ± 60.8	1.8 ± 0.3	3980.0 ± 661.4	0.1 ± 0.0
18 November 1974	142.0 ± 12.4	316.0 ± 20.9	0.4 ± 0.0	3740.0 ± 551.0	0.0 ± 0.0
13 January 1975	66.0 ± 17.2	158.0 ± 25.8	0.4 ± 0.0	1860.0 ± 405.7	0.0 ± 0.0
11 March 1975	39.2 ± 13.9	162.0 ± 15.0	0.2 ± 0.1	0420.0 ± 333.8	0.0 ± 0.0
5 May 1975	80.0 ± 24.1	80.0 ± 14.1	0.9 ± 0.0	2660.0 ± 616.9	0.0 ± 0.0
30 June 1975	110.0 ± 32.7	100.0 ± 27.1	1.2 ± 0.6	2140.0 ± 510.5	0.0 ± 0.0
25 August 1975	238.0 ± 72.0	114.0 ± 20.6	2.0 ± 0.2	4360.0 ± 872.1	0.0 ± 0.0

APPENDIX D: SUMMARY OF THE INSTANTANEOUS RATE OF DETRITUS FLUX, AMOUNT OF MATERIAL DISAPPEARING, ESTIMATED NET AERIAL PRIMARY PRODUCTION, AND ESTIMATED MORTALITY FOR THE ANGIOSPERMS SAMPLED

Collection date	r_i	X_1	X_2	P_1	P_2	M_1	M_2
			Distichlis spicata, Delaware				
27 August 1973	6.9	3.4	190.4	9.8	548.8	12.4	694.4
22 October 1973	6.4	5.2	291.2	1.8	100.8	7.4	414.4
17 December 1973	3.3	3.6	201.6	11.3	632.8	11.2	627.2
11 February 1974	1.4	1.8	100.8	-0.2	-11.2	-0.3	-16.8
8 April 1974	17.7	15.9	890.4	10.4	582.4	5.4	302.4
3 June 1974	5.7	3.3	184.8	8.1	342.6	2.9	162.4
29 July 1974	9.5	5.4	302.4	15.2	851.2	5.0	280.0
24 September 1974	8.9	6.5	364.0	-6.3	-352.8	12.9	722.4
18 November 1974	5.5	5.3	296.8	5.9	330.4	6.9	386.4
13 January 1975	1.8	1.7	95.2	-0.4	-22.4	-0.3	-16.8
11 March 1975	16.5	11.9	666.4	7.0	392.0	5.8	324.8
5 May 1975	3.1	1.4	78.4	6.8	380.8	-2.5	-140.0
30 June 1975	4.2	1.3	72.8	0.5	28.0	0.8	44.8
25 August 1975	3.7						

Collection Date	r_1	X_1	X_2	P_1	P_2	M_1	M_2
			Distichlis spicata, Georgia				
27 August 1973	-3.7	-2.0	-112.0	4.7	263.2	5.7	319.2
22 October 1973	36.3	22.9	1282.4	16.4	918.4	18.0	1008.0
17 December 1973	26.3	31.4	1198.4	32.7	1831.2	32.8	1836.8
11 February 1974	26.5	25.6	1433.6	22.3	1248.8	19.5	1092.0
8 April 1974	19.6	16.8	940.8	17.7	991.2	19.0	1064.0
3 June 1974	12.0	10.5	588.0	11.4	638.4	9.1	509.6
29 July 1974	5.4	3.9	218.4	2.0	112.0	-0.1	-5.6
24 September 1974	-4.6	-4.3	-240.8	6.9	286.4	7.3	408.8
18 November 1974	14.1	14.6	817.6	2.0	112.0	6.4	358.4
13 January 1975	3.3	2.9	162.4	4.4	246.4	5.1	285.6
11 March 1975	25.9	20.9	1170.4	16.1	901.6	16.4	918.4
5 May 1975	4.2	3.0	168.0	7.2	403.2	4.5	252.0
30 June 1975	10.6	8.6	481.6	10.4	582.4	10.2	571.2
25 August 1975	5.5						

Collection Date	r_1	Interval	X_1	X_2	P_1	P_2	M_1	M_2
			Juncus gerardii creekbank, Maine					
8 April 1975	36.9	28	19.0	532.0	23.3	652.0	21.9	614.0
5 May 1975	36.9	29	10.9	522.0	4.6	134.1	-7.1	-205.9
3 June 1975	36.9	27	1.6	43.2	10.9	293.2	2.3	61.2
30 June 1975	36.9	29	20.3	588.7	55.4	1606.7	54.7	1586.7
29 July 1975	36.9	27	27.0	1086.0	-13.2	-357.0	3.4	91.0
25 August 1975	36.9	30	22.5	675.0	29.4	883.0	35.6	1069.0
24 September 1975	5.2	197	3.3	650.0	1.6	322.1	1.6	318.1
			Juncus gerardii highmarsh, Maine					
8 April 1975	-0.8	28	-0.0	-1.2	0.1	3.4	0.1	2.8
5 May 1975	9.1	56	0.4	19.6	0.2	13.0	-0.3	-13.4
3 June 1975	24.3	29	0.8	24.0	9.1	265.0	1.7	48.0
29 July 1975	24.3	27	1.5	39.4	2.0	53.4	2.5	67.4
25 August 1975	24.3	30	6.1	184.4	13.1	394.4	18.1	542.4
24 September 1975	4.6	197	1.1	218.8	-1.2	-244.2	-0.8	-162.2

Collection date	r_1	X_1	X_2	P_1	P_2	M_1	M_2
	Juncus gerardii, Delaware						
27 August 1973							
	-9.6	-4.2	-235.2	-8.1	-453.6	-4.9	-274.4
22 October 1973							
	-2.9	-1.5	- 84.0	1.5	84.0	1.5	84.0
17 December 1973							
	4.2	2.5	140.0	3.1	173.5	2.9	162.4
11 February 1974							
	12.8	5.2	291.2	0.6	33.6	-1.9	-106.4
8 April 1974							
	27.1	7.2	403.2	15.3	856.8	9.3	520.8
3 June 1974							
	10.2	5.5	308.0	9.1	509.6	13.0	728.0
29 July 1974							
	1.2	0.8	44.8	-6.3	-352.8	-2.1	-117.6
24 September 1974							
	8.3	4.5	252.0	2.5	140.0	3.0	168.0
18 November 1974							
	3.4	1.9	106.4	3.7	207.2	3.6	201.6
13 January 1975							
	25.7	13.9	778.4	12.1	677.6	11.8	660.8
11 March 1975							
	26.8	9.9	554.4	10.7	599.2	5.8	324.8
5 May 1975							
	7.0	1.5	84.0	5.0	280.0	0.2	11.2
30 June 1975							
	-8.6	-3.1	-173.6	-1.1	- 61.6	3.3	184.8
25 August 1975							
	15.2						

Collection Date	r_1	X_1	X_2	P_1	P_2	M_1	M_2
			Phragmites communis, Delaware				
27 August 1973	0.0	0.0	0.0	- 8.4	- 470.4	4.5	252.0
22 October 1973	-47.1	-107.0	-5992.0	-51.4	-2878.4	-39.7	-2223.2
17 December 1973	- 1.7	7.3	408.8	2.3	128.8	2.3	128.8
11 February 1974	7.4	28.8	1612.8	- 0.7	- 33.6	- 0.6	- 33.6
8 April 1974	2.9	8.2	459.2	5.2	291.2	1.0	56.0
3 June 1974	6.4	15.6	873.6	20.7	1159.2	7.7	431.2
29 July 1974	- 4.0	- 9.0	- 504.0	- 9.7	- 543.2	- 7.4	- 414.4
24 September 1974	3.6	8.4	470.4	- 3.6	- 201.6	11.3	632.8
18 November 1974	-11.0	-31.9	-1786.4	-15.8	- 884.8	-15.8	- 884.8
13 January 1975	6.7	18.9	1058.4	0.4	22.4	0.4	22.4
11 March 1975	- 8.2	-24.9	-1394.4	0.6	33.6	0.2	11.2
5 May 1975	13.0	33.8	1892.8	8.6	481.6	-6.6	- 369.6
30 June 1975	- 8.4	-16.3	- 912.8	0.1	5.6	0.6	33.6
25 August 1975	3.6						

Collection Date	r_1	Interval	X_1	X_2	P_1	P_2	M_1	M_2
			Spartina alterniflora creekbank, Maine					
8 April 1975								
	38.4	28	1.2	68.2	2.1	59.0	1.6	44.8
5 May 1975								
	38.4	29	1.2	35.0	6.3	183.6	2.0	57.8
3 June 1975								
	38.4	27	1.7	45.5	8.8	236.3	1.8	47.7
30 June 1975								
	38.4	29	10.0	290.9	19.5	564.7	15.9	462.1
29 July 1975								
	38.4	27	6.9	186.2	1.9	51.2	4.1	112.8
25 August 1975								
	38.4	30	11.0	331.1	15.4	461.3	20.7	619.9
24 September 1975								
	13.5	197	3.2	631.9	0.2	32.5	1.2	243.5
			Spartina alterniflora highmarsh, Maine					
8 April 1975								
	-3.8	28	-2.2	-60.7	-1.1	-29.9	-1.2	-22.7
5 May 1975								
	16.3	29	8.2	239.2	5.2	152.2	2.9	82.8
3 June 1975								
	16.3	27	5.0	135.3	2.1	55.7	-3.9	-105.3
30 June 1975								
	16.3	29	4.5	130.7	11.1	321.1	10.7	309.7
29 July 1975								
	16.3	27	5.0	134.3	3.2	85.4	4.2	113.8
25 August 1975								
	16.3	30	7.2	216.3	17.6	528.5	20.4	612.7
24 September 1975								
	8.5	197	5.1	1002.9	4.0	786.5	4.7	919.5

Collection Date	r_i	X_1	X_2	P_1	P_2	M_1	M_2
			Spartina cynosuroides, Georgia				
27 August 1973							
	- 7.0	- 4.8	-268.8	3.3	184.8	9.5	532.0
22 October 1973							
	32.6	41.8	2340.8	28.3	1584.8	48.6	2721.6
17 December 1973							
	6.4	11.1	621.6	20.5	1148.0	20.2	1131.2
11 February 1974							
	- 1.2	- 2.7	-151.2	7.8	436.8	2.7	151.2
8 April 1974							
	17.0	30.4	1702.4	32.0	1792.0	2.8	716.8
3 June 1974							
	2.2	2.4	134.4	-0.9	-50.4	-4.1	-229.6
29 July 1974							
	-38.9	-40.6	-2273.6	-44.2	-2475.2	-36.5	-2044.0
24 September 1974							
	64.6	103.2	5779.2	99.1	5549.6	118.7	6647.2
18 November 1974							
	1.3	2.7	151.2	1.2	67.2	3.1	173.6
13 January 1975							
	10.4	19.9	1114.4	17.8	996.8	14.9	834.4
11 March 1975							
	1.6	2.6	145.6	6.5	364.0	-5.6	-313.6
5 May 1975							
	18.0	22.7	1271.2	44.3	2480.8	20.4	1142.4
30 June 1975							
	10.4	19.7	1103.2	30.0	1680.0	44.5	2492.0
25 August 1975							
	10.0						

Collection Date	r_1	X_1	X_2	P_1	P_2	M_1	M_2
			Spartina patens, Delaware				
27 August 1973							
	12.4	8.2	459.2	3.5	196.0	2.5	140.0
22 October 1973							
	52.8	30.2	1691.3	15.6	873.6	32.7	1831.2
17 December 1973							
	-0.8	-0.6	-33.6	2.3	128.8	1.0	56.0
11 February 1974							
	4.4	2.8	156.8	-2.0	-112.0	-1.5	-84.0
8 April 1974							
	11.4	5.1	285.6	3.9	218.4	1.9	106.4
3 June 1974							
	5.2	3.5	196.0	16.7	935.2	14.3	800.8
29 July 1974							
	5.5	4.8	268.8	3.3	184.8	1.9	106.4
24 September 1974							
	11.7	9.1	509.6	4.6	257.6	8.2	459.2
18 November 1974							
	4.8	3.7	207.2	3.6	201.6	4.0	224.0
13 January 1975							
	10.5	8.4	470.4	7.8	436.8	9.3	520.8
11 March 1975							
	16.0	13.2	739.2	15.3	856.8	13.3	744.8
5 May 1975							
	10.4	6.3	352.8	2.1	117.6	-1.6	-89.6
30 June 1975							
	10.9	5.1	285.6	13.9	778.4	8.1	453.6
25 August 1975							
	3.0						

Collection Date	r_1	X_1	X_2	P_1	P_2	M_1	M_2
			Spartina patens, Georgia				
27 August 1973							
	5.6	2.4	134.4	3.4	190.4	2.0	112.0
22 October 1973							
	8.0	4.4	246.4	5.3	296.8	8.8	492.8
17 December 1973							
	17.6	11.3	632.8	20.0	1120.0	10.4	582.4
11 February 1974							
	20.1	16.2	907.2	23.8	1332.8	22.7	1271.2
8 April 1974							
	30.3	25.2	1411.2	12.4	694.4	19.9	1114.4
3 June 1974							
	-1.3	-0.8	-44.8	-2.9	-162.4	-2.6	-145.6
29 July 1974							
	5.7	2.7	151.2	-3.8	-212.8	-1.2	- 67.2
24 September 1974							
	-1.0	-0.6	-33.6	7.1	397.6	9.3	520.8
18 November 1974							
	28.2	23.5	1316.0	20.2	1131.2	20.3	1136.8
13 January 1975							
	11.0	5.4	302.4	-5.3	-296.8	-3.6	-201.6
11 March 1975							
	4.0	2.4	134.4	20.2	1131.2	20.3	1136.8
5 May 1975							
	7.0	8.1	453.6	22.9	1282.4	14.2	795.2
30 June 1975							
	25.8	29.8	1168.8	18.4	1030.4	23.7	1327.2
25 August 1975							
	0.9						

Collection Date	r_i	Interval	X_1	X_2	P_1	P_2	M_1	M_2
			Spartina patens, Maine					
8 April 1975								
	16.4	28	25.2	706.7	--	400.7	14.3	400.7
5 May 1975								
	16.4	29	28.8	834.7	--	1636.7	54.2	1572.7
3 June 1975								
	16.4	27	25.7	694.8	--	-257.2	-26.5	-715.2
30 June 1975								
	16.4	29	24.9	722.9	--	2078.9	59.8	1734.9
29 July 1975								
	16.4	27	17.7	477.8	--	-1370.2	-52.5	-1416.2
25 August 1975								
	16.4	30	21.9	657.8	--	1518.8	57.7	1730.8
24 September 1975								
	3.1	197	9.0	1796.2	--	1556.2	11.5	2256.2

Collection Date	r_i	X_1	X_2	P_1	P_2	M_1	M_2
	Sporobolus virginicus, Georgia						
27 August 1973							
22 October 1973							
17 December 1973							
11 February 1974							
	32.6	7.5	420.0	8.4	470.4	6.3	352.8
8 April 1974							
	35.9	8.3	464.8	9.0	504.0	9.5	532.0
3 June 1974							
	17.5	3.5	196.0	1.5	84.0	1.3	72.8
29 July 1974							
	25.2	4.1	229.6	6.5	364.0	4.8	268.8
24 September 1974							
	-2.5	-0.6	-33.6	-0.3	-16.8	1.8	100.8
18 November 1974							
	17.0	4.0	224.0	-0.1	- 5.6	1.2	67.2
13 January 1975							
	2.3	0.4	22.4	0.0	0.0	0.4	22.4
11 March 1975							
	42.5	5.2	291.2	4.5	252.0	3.7	207.2
5 May 1975							
	66.5	6.1	341.6	6.9	386.4	6.4	358.4
30 June 1975							
	2.7	0.3	16.8	2.8	156.8	0.5	28.0
25 August 1975							
	13.9						

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